PL. LIX.

Last larval stage (*Mysis* stage) of *Limnocaridina parvula* Clm.

Fig. 1. Dorsal view of the larva.
2. Same larva, viewed from left side.
3. Antennula.
4. Antenna.
5. Anterior lip.
6. Right mandible and masticatory part of left.
7. Anterior maxilla.
8. Posterior maxilla.
9. Maxilliped of 1st pair.
10. Maxilliped of 2nd pair.
11. Maxilliped of 3rd pair.
12. Cheliped (exopodite not fully drawn).
13. Pereiopod of 1st pair (exopodite not fully drawn).
14. Pereiopod of last pair.
15. Pleopod of 1st pair.
16. Pleopod of 2nd pair.
17. Extremity of last caudal segment, with telson and left uropod; dorsal view.

PL. LX.

First post-larval stage of *Limnocaridina parvula* Clm.

Fig. 1. Dorsal view of the specimen.
2. Same specimen, viewed from left side.
3. Antennula.
4. Antenna.
5. Mandible.
6. Anterior maxilla.
7. Posterior maxilla.
8. Maxilliped of 1st pair.
9. Maxilliped of 2nd pair.
10. Maxilliped of 3rd pair.
11. Cheliped.
12. Pereiopod of 1st pair.
13. Pereiopod of last pair.
14. Pleopod.
15. Outer part of telson.

25. The Classification, Morphology, and Evolution of the Echinoidea Holectypoida. By HERBERT L. HAWKINS, M.Sc., F.G.S.; Lecturer in Geology, University College, Reading*.

[Received November 16, 1911: Read March 5, 1912.]

(Text-figures 54–60.)

CONTENTS.

I. INTRODUCTION.

Within the limits of a single class, it would be difficult to find greater contrasts than those which distinguish the various orders

* Communicated by Dr. HENRY WOODWARD, F.R.S., V.P.Z.S.

of the Echinoidea. To a casual observer, unacquainted with the anatomy and embryology of the forms, such genera as *Cidaris* and *Echinocardium* would seem to represent two absolutely different "kinds" of animals. Moreover, search as he might among the Echinoids of the present day, he could find no types that would effectively bridge the gulf that separates the Regular from the Irregular Sea-Urchins. All the Regularia have thick tests, built on a radially symmetrical plan; possess a strong jaw-apparatus; and are armed with stout, often very long, radioles. On the other hand, most of the Irregularia have thin tests, bilaterally symmetrical; have no jaws; and are covered with small, almost hair-like radioles. Even those forms, the "Cake-Urchins," which show a radial symmetry and possess jaws, have other characters which render them very different in appearance from the Regular Echinoids.

And again, from an anatomical study of living forms alone, although a similarity of structure sufficient to warrant their inclusion in the same order of the Echinoderma might be found, no certain clues as to the relation of the two types to one another could be discovered. Even ontogenetic evidence is lacking to a considerable degree, for the peculiar larval life led by Echinoids has tended to neutralise the effect of recapitulation.

At this point, where Zoology in its narrower sense fails, Palæontology can supply the connecting links between such different forms as a Cidarid and a Spatangid; and of these links, the majority are to be found in the group which forms the subject of this research. The order Holectypoida arose soon after the commencement of the Jurassic period, and became entirely extinct before the close of the Mesozoic era. During its existence it gave rise to forms which, by stages so gradual as to be hardly distinguishable, laid the foundations of all the great groups of Irregular Echinoids that are living to-day. It is the purpose of this paper to indicate in outline the processes through which the specialization of Clypeastroids, Spatangoids, and "Cassidulids" was achieved.

When P. M. Duncan (**44**)* wrote his classic "Revision of the Genera and great Groups of the Echinoidea," there existed "much diversity of opinion regarding the nature of the perignathic girdles and jaws of some genera" (*t.c.*, p. 135) of the Holectypoida, the most primitive group of the Irregular Echinoids. As Duncan's system of classification was based to a very large extent on the varying characters of these structures, it naturally resulted that in the case of the Holectypoida and their allies the grouping of genera into families, or even into larger groups, was somewhat tentative. It is only necessary to remark that jaws are now known to have existed in two genera, in which their presence was denied by Duncan, to show that a revision of the classification of the group is required.

* Where a number in brackets follows the name of an author, the full title of the paper referred to will be found under that number in the chronological list of literature at the end of this paper.

However, the difficulties of a systematic grouping of the primitive gnathostomatous Irregularia are not removed, or even lessened, by the additions that have been made to our knowledge of their comparative anatomy. Rather are they increased, for the establishment of affinities between genera leads to greater complexity of classification than that of differences. The Holectypoida are an annectant group, the history of whose evolution is so intimately interwoven with that of the early stages of most of the Irregular orders and suborders, that to frame a purely natural classification would need an impracticable plasticity of diagnoses. This systematic trouble is, however, more than compensated by the phylogenetic evidence that it indicates. In the course of the following work I have endeavoured, while recasting the artificial classification of the systematist, to lay emphasis on relationships rather than on contrasts, and to show the position occupied by the Holectypoida at the foundation of the varied structures of the Irregular Echinoids.

The present essay is the outcome of several years of study of the group, and contains a summary and amplification of a series of papers (see list at end) that have been published in the 'Geological Magazine.' I have thought it unnecessary to repeat here many of the details described in those papers, so that, except where corrections or additions have been possible, the results arrived at in them are taken for granted. There are, however, descriptions of a number of features that find a place here which were not dealt with in the shorter papers given here.

After a brief sketch of the history of the classification of the group, the revised scheme is put forward. This is followed by a morphological comparison of the genera within, and of some genera without, the boundaries of the order; and lastly, the directions of evolution thus indicated are discussed.

II. History of Past Classification.

This part of the paper does not pretend to be a complete account of all the past work that has been done on the group, but it is a summary of the chief systems of classification that have been proposed up to the present time.

The history of the group may be said to date from 1734, when Klein, in his 'Naturalis dispositio Echinodermatum,' distinguished "Sectio I, *Fibula*," from the rest of the "*Echini catocysti circulares*." The section was diagnosed as follows:—"*Echinos fibulares* dicimus *Catocystos* circa Basis circularis peripheriam *Anum*, *Os* in medio aperientes." He included two genera only in the section, *Conulus* and *Discoides*, both of which are recognized to-day, and have been associated with one another in most of the systems of classification. Klein apparently did not know of any of the other genera included among the Holectypoida in the present paper.

The classification adopted in 1840 by L. Agassiz, in his 'Catalogus systematicus,' was in many ways of less value than that of Klein; for he grouped together, under the heading of "Clypeastroidæ," all the non-Spatangid Irregular Echinoids. However, Desor, in the sequel to that Catalogue (**11**) showed that a more detailed system of subdivision was practicable, and founded the first definite scheme of the classification of the group. The "tribu" of the "Galérites" was regarded as a division of the "Clypéastroides." It contained the following genera:—*Caratomus*, *Discoidea*, *Echinoneus*, *Galerites*, *Globator*, *Holectypus* (as a subgenus of *Discoidea*), *Hyboclypus*, *Nucleopygus*, *Pygaster*, and *Pyrina*. This list of genera contains a very natural grouping of all those Irregular Echinoids which have simple, apetaloid ambulacra. That, however, is almost the only trait that could associate them, and in *Caratomus*, at least, the simplicity of the ambulacra is not absolute.

In the 'Catalogue raisonnée' (1847) Agassiz and Desor retained this grouping of the genera in its entirety, but rearranged the position of the "tribu" as a whole. It appears as the family Echinoneidæ, a section of the Cassidulidæ. This change was at once an advance and a retrogression. It applied to the family a name under which some of the genera have remained since that time, but by associating the whole series with the Cassidulids, it tended to obscure the importance of the gnathostomatous character of many of the genera.

In the Synopsis, Desor (**21**) retained the division under the name of Galeridées, and added large numbers of genera to the list. He recognized, however, the fundamental importance of the presence of jaws in determining the systematic position of a genus, and so separated the Galeridées into two groups. Of these, the first, or "Galeridées proprement dits," contained fifteen genera with jaws (or rather, supposed to possess them), while the second, the "Echinonées," included *Echinoneus* only. The first group contained all the genera of the "Galérites" of 1842, except *Caratomus* and *Echinoneus*, and there were added the then newly described genera *Anorthopygus*, *Asterostoma*, *Desorella*, *Galeropygus*, *Pachyclypus*, and *Pileus*. It is curious that Desor should have taken it for granted that all these fossil genera were gnathostomatous, for he cannot have had any positive evidence to work upon in the majority of cases.

In 1857 Pictet, in the second edition of his 'Paléontologie' (**22**), reverted to the method of grouping originated by Desor in 1842, changing the word "Galérites" to the subordinal term "Galeritiens," and adding the then recently described *Desoria*.

One year before the appearance of Desor's Synopsis, Wright (**20**) had grasped the essential differences which divided the "Galérites" into two sections. He founded the family of the Echinoconidæ, which contained *Discoidea*, *Echinoconus* (the *Galerites* of most previous authors), *Holectypus*, *Hyboclypus*, and

Pygaster. He contrasted this family with the Echinoneidæ, in which he placed *Echinoneus*, *Pyrina*, and several other genera. This was the first time that the presence of jaws was treated as an essential feature in the classification of the group.

Wright's system of classification was adopted for many years by almost all the Echinologists who dealt with the group, although slight changes in the generic personnel of the Echinoconidæ were introduced. Cotteau (28) removed *Hyboclypus*, with good reason, from the family, and added the genera (unknown to Wright in 1856) *Anorthopygus* and *Pileus*.

The compact group thus determined, bound together by the characters of a short and accurate diagnosis, became generally accepted. Lovén (**31**) worked on this classification as a basis, and Wright (**32**) agreed with Cotteau's modifications. Perhaps no surer indication of the natural character of the grouping could anywhere be found than in the fact that Pomel (**37**) was unable to find any cause for more than internal changes in the family.

With a subordinal rank within the group of Gnathostomes Clipéiformes, Pomel placed the section Galérides. This section he subdivided into two chief families, the Echinoconidés and the Piléidés. The latter family was further separated into two subfamilies, the Discoidiens and the Pygasteriens. Although many new "generic" terms were introduced, no forms were included among the Galérides that were not previously classed with the Echinoconidæ. The separation of the *Echinoconus*-group from the other genera was natural. In the Piléidés, the first group was simply the original genus *Discoidea* of Agassiz in a dismembered state, while the second group included the same author's early conception of the genus *Pygaster*. The classification of Pomel was therefore, in this group, quite orthodox, a condition of affairs sufficiently surprising in view of the great changes he proposed in the arrangement of many of the other groups.

In 1889, Duncan (**44**), who expressly dissociated himself from Pomel's views of the relative importance in classification of various structures, published the invaluable Revision of the Genera, etc. of Echinoidea. In this work, he realised the great importance of the Holectypoida as an annectant group. So thoroughly intermediate in its characters was the group that he definitely stated that his classification was artificial, and as such tentative. The Holectypoida received the rank of an Order, equivalent in importance to the Clypeastroida or the much larger groups of the Diademoida and Spatangoida.

It was chiefly on the peristomial and jaw-structures that Duncan classified the group, and on that account it was particularly unfortunate that he should have had such a fixed belief in the absence of jaws in some genera in which they have since been discovered. Curiously enough, although, in the same year as the publication of the Revision, he definitely stated his disbelief in the existence of jaws in *Discoidea* (**45**), he allowed that genus to find a place among the Holectypoida, while *Echinoconus* was banished to the Echinoneidæ among the Spatangoida. A similar fate befell *Anorthopygus*, while *Conoclypeus*, a genus till then usually classed with either *Echinanthus* or *Clypeaster*, was brought into the Holectypoid group. (*Conoclypeus* was regarded as a "*Galerites*" by Grateloup, **5**.)

Duncan divided the Holectypoida (whose brief diagnosis was "Exocyclic, oligoporous Ectobranchiata") into two unnamed sections. The subdivision was made on the details of the perignathic girdle, and *Discoidea* and *Conoclypeus*, on account of the supposed rudimentary state of their processes, were thus separated from *Holectypus* and *Pygaster*. *Galeropygus* and *Pachyclypeus* were regarded as being Holectypoids, but as not sufficiently known to be definitely associated with, or separated from, any of the other genera.

Duncan's classification was followed absolutely by Sladen in the "Zittel-Eastman" Text Book of Palæontology (**53**).

The only remaining classification of the group in which any important changes are made is that devised by Gregory in 1896 (**50**), and published in Lankester's 'Treatise on Zoology.' Here the "Holectypina" (a group corresponding in part with the Holectypoida) are regarded as a suborder of the Gnathostomata. The chief contrast between Gregory's group and that of Duncan, is that the former author so modifies the diagnosis of the Holectypina as to admit *Galerites* (*Echinoconus*), although it is believed to be edentulous. The Holectypina are divided into four families, the Pygasteridæ, the Discoidiidæ, the Galeritidæ, and the Conoclypeidæ. Discounting the genera described since 1889, the Pygasteridæ correspond to section I. of the Holectypoida, with the queried inclusion of *Galeropygus* and *Pachyclypeus*. The Discoidiidæ and Conoclypeidæ together contain the members of Duncan's second section, while the Galeritidæ are the first subfamily of the Echinoneidæ of the Revision.

The classification proposed by Gregory seems to accord better with our knowledge than any of those previously suggested. In view of the complexity of the relations of the Holectypoida, owing to its primitive and annectant character, I prefer to regard it as a group so much apart from the other Irregularia as to merit its retention as an Order, as Duncan originally considered it. After a thorough study of the comparative morphology of most of the genera included in the order, I have attempted to revise its internal classification in such a manner as to indicate the affinities, both internal and external, which the study has made manifest.

III. The Revised Classification.

The characters of an annectant group are inevitably plastic and unstable. For this reason a natural classification of such a group becomes an almost impossible task. The features which seem of essential importance in one genus may be quite absent or profoundly modified in another. But in the case of the Holectypoida, the length of time during which this plasticity of structure was retained gives possibility for a classification that is fairly in accord with the evolution of the group, and at the same time is free from a confusing multiplicity of detail. However, as will be seen on a comparison of the scheme submitted below with the genealogical table given in a later part of the paper, the two groupings do not agree in every particular. All of the genera have a great phylogenetic significance, and would, if the classification were to do justice to that importance, require each a separate family. Probably, as our knowledge of the relations of the group extends, the present genera will become the bases of distinct families, and will be themselves divided into many smaller sections. The great variety of species which are at present grouped under the generic names *Holectypus* and *Discoidea* seems to lend support to this belief. For convenience of reference, it has seemed preferable to retain, as far as possible, a more generalized system of grouping than, by comparison with other orders of Echinoidea, the individual peculiarities of the genera in reality demand.

The Holectypoida are an order intermediate in characters between the Echinoidea Regularia and all the various orders of the Irregularia. The features in their structure which are naturally the most uniform in character are therefore those relics of "Regularity" that they retain. They show a persistently retarded progress in their evolution, and from them, at various points, relatively accelerated offshoots break free. Throughout the entire group two features remain constant in their presence, although they undergo a gradual reduction in the perfection of their development. These features are:—the existence of a masticatory apparatus; and the presence of external peristomial branchiæ. Both of these structures are of essential importance physiologically, and both fortunately leave traces of their existence on the skeletal structures. It is a postulate (which probably expresses a fact) that, whenever the peristome is centrally situated, and at the same time circular in outline, jaws are present. Certainly the existence of a well-developed perignathic girdle indicates their presence, so that, when either of these characters can be observed, the existence of a masticatory apparatus can be inferred, even if it has not been discovered. The branchial incisions on the peristome margin are naturally easy to recognize when that part of the test is preserved.

After the scheme of classification has been summarized, revised diagnoses will be given for the order, families, and genera. Subsequently, the reasons for the exclusion of some genera which have hitherto been classed with the Holectypoida will be discussed, and their positions in the other orders indicated.

Order HOLECTYPOIDA.

Family I. PYGASTERIDÆ.

Subfamily 1. Pygasterinæ.

Genus Pygaster Agassiz.

Subgenus 1. *Pygaster* sens. str.
" 2. *Megapygus*, nom. nov.
" 3. *Macropygus* Cotteau.

Subfamily 2. Pileinæ.

Genus 1. Pileus Desor.
" 2. Anorthopygus Cotteau.

Family II. DISCOIDIIDÆ.

Subfamily 1. Holectypinæ.

Genus 1. Holectypus Desor.

Subgenus 1. *Holectypus* Desor.
" 2. *Cœnholectypus* Pomel.
" 3. *Lanieria* Duncan.

Genus 2. Coptodiscus Cotteau & Gauthier.

Subfamily 2. Discoidiinæ.

Genus Discoidea Agassiz.

Family III. CONULIDÆ.

Genus Conulus Leske.

Incertæ sedis:—Discholectypus Pomel.

Order HOLECTYPOIDA Duncan (emend.).

Euechinoidea Irregularia with external peristomial branchiæ (Ectobranchiata) and a central mouth armed with jaws and surrounded by a perignathic girdle (Gnathostomata).

Ambitus circular, subpentagonal, posteriorly truncated, or slightly elongated. Adapical surface acutely or bluntly conical, apex practically central. Peristome central, usually circular, sometimes decagonal or even obliquely elliptical in outline. Perignathic girdle discontinuous, composed of both processes and ridges. Jaws more like those of the Regularia than of the Clypeastroida. Periproct very variable in size and position, always posterior.

Ambulacra straight, narrow, similar, and simple, with usually larger podial pores on the adapical than on the adoral surface. Towards the peristome the pore-pairs may become grouped into arcs of three. Ambulacral plates small, simple or compound, the latter always derived from three original primary plates. Interambulacra broad; the plates usually concentric in arrangement, rarely bent along their median line. Tubercles always in recognizably vertical series. Apical system variable; madreporite usually large. Radioles short, and longitudinally striated.

Liassic to Uppermost Cretaceous.

Family I. PYGASTERIDÆ.

Holectypoida with a circular or posteriorly truncated ambital outline. Bluntly conical adapically, concave adorally. Peristome large, with strong perignathic processes and feeble ridges. Jaw-structure insufficiently known for diagnosis. Branchial incisions deep. Periproct large, always on the adapical surface, often oblique. Ambulacra slightly tumid, composed of primaries to a point about midway between the ambitus and the peristome. Outer members of pore-pairs often transversely elongated (to a slight degree only) on the adapical surface. Interambulacra broad, paucituberculate (for an Irregular Echinoid), the admedian tubercles being in concentric series, the adradial oblique. Granulation irregular, faintly scrobicular. Apical system with four perforated genital plates; the fifth being usually represented by several small plates. Ocular plates small and similar. No internal buttresses to the test. Radioles short, longitudinally striated.

Liassic to Lower Cretaceous.

Subfamily 1. PYGASTERINÆ.

Pygasteridæ with the periproct in contact with the apical system. Ambulacral pore-pairs uniserial except near the peristome.

Genus 1. PYGASTER Agassiz.

With the characters of the subfamily.

Genotype, *P. semisulcatus* Phillips.

Subgenus 1. PYGASTER sens. str. (=*Plesiechinus* Pomel).

Pygaster with the periproct inside, as well as outside, the apical system, and with its greatest width in the adapical part. No posterior genital plate, the remaining plates of the system being arranged transversely. Tubercles with shallow scrobicules, regular in their introduction.

Subgenotype. *P. semisulcatus* Phillips.

Liassic to Middle Oolitic.

Subgenus 2. MEGAPYGUS nov. (*Pygaster* restr. Pomel).

Pygaster with periproct pyriform, and constricted towards the apex. Fifth genital plate present, or replaced by several small plates. Tubercles with shallow scrobicules and irregular in their introduction.

Subgenotype. *M. umbrella* (auctt.).

Middle and Upper Oolitic.

Subgenus 3. MACROPYGUS Cotteau.

Pygaster with the periproct and apical system as in *Megapygus*. Posterior margin strongly truncated. Tubercles with large, deep scrobicules; regular in their introduction.

Subgenotype. *M. truncatus* Agassiz.

Lower Oolitic to Lower Cretaceous.

Subfamily 2. PILEINÆ.

Pygasteridæ with the periproct midway between the apex and the ambitus. Madreporite very large, occupying the centre of the apical system.

Genus 1. PILEUS Desor.

Pileinæ with the ambulacral pore-pairs biserial adapically. Periproct very slightly oblique. Fifth genital plate small, imperforate.

Genotype. *P. pileus* Agassiz.

Corallian.

Genus 2. ANORTHOPYGUS Cotteau.

Pileinæ with the ambulacral pore-pairs uniserial throughout. Periproct markedly oblique. Apical system ethmolysian. Tubercles of interambulacra in sloping lines on both sides of the central series.

Genotype. *A. orbicularis* Grateloup.

Lower and Middle Cretaceous.

Family II. DISCOIDIIDÆ.

Holectypoida with a circular or posteriorly elongated ambital outline. Depressed or elevated, conical, adapically; flat or slightly concave adorally. Peristome of moderate size, with strong perignathic processes and well-developed ridges. Branchial incisions well marked. Periproct of variable size, marginal or adoral in position. Ambulacral plates primaries to the ambitus, compound there and adorally. Pores usually equal and circular. Interambulacra broad, with many vertical rows of tubercles, often supplemented by hypertrophied granules. Granulation usually transversely linear. Tubercles much larger on the adoral than on the adapical surface; arrangement as in

Pygasterinæ. Apical system composed of five genital plates, the posterior one perforated or not. Madreporite central. Ocular plates often very small. Radioles short, acuminate, longitudinally striated.

Lower Oolitic to Upper Cretaceous.

Subfamily 1. HOLECTYPINÆ.

Discoidiidæ with the periproct marginal or adoral in position. Fifth genital plate smaller than the other four. Tuberculation usually sparse. Perignathic ridges low. No internal buttresses to the test.

Genus 1. HOLECTYPUS Desor.

Holectypinæ with the characters of the subfamily.

Genotype. *H. depressus* Leske.

Subgenus 1. HOLECTYPUS sens. str.

Holectypus with the posterior margin often elongated; with a large periproct, marginal or adoral in position. Fifth genital plate small and imperforate. Madreporite central and prominent.

Subgenotype. *H. depressus* Leske.

Lower and Upper Oolitic.

Subgenus 2. CŒNHOLECTYPUS Pomel.

Holectypus with a circular ambitus; periproct of comparatively small size, usually adoral in position. Fifth genital plate almost as large as the others, and perforated.

Subgenotype. *C. macropygus* Desor.

Lower to Upper Cretaceous.

Genus 2. COPTODISCUS Cotteau & Gauthier.

Holectypinæ similar to *Cœnholectypus*, but with deep excavations along the plate sutures on the adapical surface.

Genotype. *C. nœmiœ* Cott. & Gauth.

Genus 3. LANIERIA Duncan.

Holectypinæ similar to *Cœnholectypus*, but globular in shape.

Genotype. *L. lanieri* d'Orbigny.

Upper Cretaceous.

Subfamily 2. DISCOIDIINÆ.

Discoidiidæ with a circular ambitus; with the periproct on the adoral surface. All five genital plates of approximately equal size, the posterior plate perforated or not. Madreporite often scattered over all five genitals. Perignathic ridges high. Internal buttresses present on the adoral surface.

Genus 1. Discoidea Agassiz.

With the characters of the subfamily.

Genotype. *D. subucula* Leske.

Lower and Upper Cretaceous.

Family III. CONULIDÆ.

Holectypoida with a posteriorly elongated or circular ambital outline. Usually tall and conical adapically; flat or subconvex adorally. Peristome small, slightly elliptical and sometimes oblique, with the perignathic ridges of equal height with the processes, the whole girdle leaning against an internally thickened portion of the adoral surface. Branchial incisions very slight. Periproct small, marginal. Ambulacra of compound plates almost throughout, pore-pairs definitely triserial near the peristome. Interambulacra multituberculate, with both admedian and adradial series sloping adorally, and often in linear sets of three instead of two on each plate. Granulation irregular, granules sunken on the adapical surface. Apical system with four genital plates only. The two posterior oculars meet along the middle line, and are larger than the other three. No internal buttresses, but a marked thickening of the interradial parts of the adoral surface. Radioles similar to those of Discoidiidæ; but in addition short ? pedicellaria-stumps arising from the invaginated granules.

Lower to Upper Cretaceous.

Genus 1. Conulus Leske.

With the characters of the family.

Genotype. *C. albogalerus* Leske.

Lower and Upper Cretaceous.

Incertæ sedis.

Discholectypus Pomel.

Holectypoida with the characters of *Cœnholectypus* except in the ambulacra, which are composed of compound plates throughout, as in the Conulidæ.

Genotype. *D. meslei* Gauthier.

Lower Cretaceous.

Discussion of the Systematic Position of Genera formerly included among the Holectypoida, but now removed from the Group.

Plesiechinus Pomel.

This genus (or subgenus) included *Pygaster semisulcatus* Phill. and other species related to it. As *P. semisulcatus* is the type of *Pygaster* Agass. (6), the name *Plesiechinus* cannot be retained. I have, therefore, renamed Pomel's subgenus *Pygaster* sens. str. The "*Pygaster*" of Pomel thus requires a new subgeneric name. As this group, which is typified by *P. umbrella*, is similar in the character of the periproct to *Macropygus*, and seems to mark a parallel though distinct line of evolution to that subgenus, I have named it *Megapygus*.

PYGASTRIDES Lovén.

As was realised from the first, this small recent form possesses all the essential features of a *Pygaster*, and the species (*P. relictus*) was originally given that generic name by Lovén. There is no direct evidence, so far as I have been able to gather it, whereby this genus should be omitted from the Pygasteridæ. But there is a serious doubt as to its being a "genus," in the strict sense of the word. It is founded on one broken and minute specimen. On first principles, the great lapse of time, unbridged by any similar forms, which separates *P. relictus* from even the latest members of the Holectypoida, renders it improbable that it can be a revived example of the group. Moreover, there has recently come to light some indirect evidence which seems thoroughly to undermine the foundations of the "genus." The presence of a generally *Pygaster*-like facies, and of a complete lantern, in a small recent Echinoid known to belong to the genus *Echinoneus* (Agassiz, 58), in addition to the extraordinary interest of its mere existence, makes it practically certain, to my mind, that the specimen described by Lovén was a similarly atavistic post-larval form. For this reason, I have thought it best to ignore *Pygastrides* in the diagnosis of the Holectypoida, and to omit it altogether from the classification.

GALEROPYGUS Cotteau (Desor).

Several well-marked features render it impossible, as well as unnatural, to associate this genus with the Pygasteridæ. Two striking differences are the strong curvature of the two posterior ambulacra at their adapical extremities (and the extreme narrowness of the areas generally), and the irregularly multituberculate character of the interambulacra. Moreover, the peristome is small, unnotched for branchiæ, and placed anteriorly from the centre. It must be regarded as the earliest known genus of the Nucleolitidæ of Gregory (50), and its affinities will be more fully discussed in Section VI. of the present paper.

ECHINITES Duncan (*Protocyamus* Gregory).

Bather has shown (55) that this "genus" (renamed by Gregory in 1900), being founded on *Discoidea subucula* Leske, must be considered a simple synonym of *Discoidea*. *D. subucula* is the type of the genus.

Conulopsis, gen. nov.*

The following is a brief diagnosis :—Ambitus circular, or very slightly elongated posteriorly; adapical surface conical, not very elevated; adoral surface flat or slightly concave. Peristome small, slightly excentric, surrounded by interradial "bourrelets." Periproct marginal or inframarginal, transversely expanded. Ambulacra of simple primaries, large adorally; pores almost subpetaloid adapically. Interambulacra multituberculate, tubercles not in vertical series, deeply scrobiculate, imperforate. Granulation coarse, closely packed.

Genotype. *C. roemeri* d'Orbigny, sub *Galerites.*

Upper Cretaceous.

This genus corresponds with the "*Echinoconus*" of Desor (**21**), but is certainly not a member of the Holectypoida. "*Galerites roemeri*" is not a "*Galerites*" at all, but, like the "*Echinoconus abbreviatus*" of our own uppermost Cretaceous (its probable congener), seems to be a near ally of *Caratomus* (see Schlueter, **54**), but to be sufficiently distinct to demand a new generic name. A further discussion of the affinities of *Conulopsis* will be found on p. 491.

Adelopneustes Gauthier.

This genus is founded on one specimen, *A. lamberti*, from the Upper Chalk of Tunis. It is compared by Gauthier (**46**) with *Galerites roemeri* d'Orbigny, and the comparison, judging by the figures, seems justified. It must therefore follow *Conulopsis* to the *Caratomus*-group.

Conoclypeus Agassiz.

There are two noteworthy features which separate this genus from the Holectypoida. There are no branchial incisions on the margin of the peristome, and the ambulacra are definitely subpetaloid. Moreover, the interambulacral tubercles are closely packed, without any recognizable vertical arrangement. *Conoclypeus*, and with it probably *Oviclypeus* Dames, represents the most primitive family of the Clypeastroida. The family name of Conoclypeidæ used by Gregory (**50**) may be retained for these two genera.

Amblypygus Agassiz.

This genus has not, so far as I am aware, been previously associated with the Holectypoida, but its affinities with that order are at least as well marked as those of the genus last mentioned. It is certainly edentulous, and the tubercles are quite irregularly packed together on the interambulacra. The ambulacra, however, in spite of an appreciably subpetaloid development on the

* A more detailed account of the characters of this genus will be given in a paper that I hope to publish shortly.

adapical surface, have exactly the plating-characters of *Conulus*. *Amblypygus* seems to represent the simplest form of the Tertiary-Recent section of the "Cassidulidæ" (see Hawkins, **66**), which is characterized by *Echinolampas* and its allies. The genus will receive fuller consideration in Section VI. of the present paper.

IV. Comparative Morphology.

Throughout this part of the paper references are made chiefly to the structures of the four common British representives of the group (*Pygaster*, *Holectypus*, *Discoidea*, and *Conulus*). Only when peculiar characters or important contrasts occur in the less abundant or foreign genera is a description of them inserted. I have followed this principle advisedly, because, as this work is largely one of generalization, it seemed preferable to use forms where plenty of material was available, rather than to run the risk of laying too strong an emphasis on a feature which, occurring in an uncommon type, might be an individual peculiarity.

A. The proportions of the Test.

1. *The circumference.*

All the forms which are included in the Holectypoida have typically a radially symmetrical outline around the ambitus. In some of the earlier forms, notably in varieties of *Pygaster semisulcatus*, there is a tendency for the outline to be quite sharply pentagonal by reason of the prominence of the ambulacra, but outside the borders of *Pygaster* sens. lat. this feature rarely appears. It is perhaps worth noting, in this respect, that among the markedly pentagonal forms in my collection of the species just mentioned, there are many of quite small size. Although thus apparently a constant feature throughout life in some individuals, the angularity seems not to represent any phylogenetic stage, but to be merely an irregular, though frequent, variation.

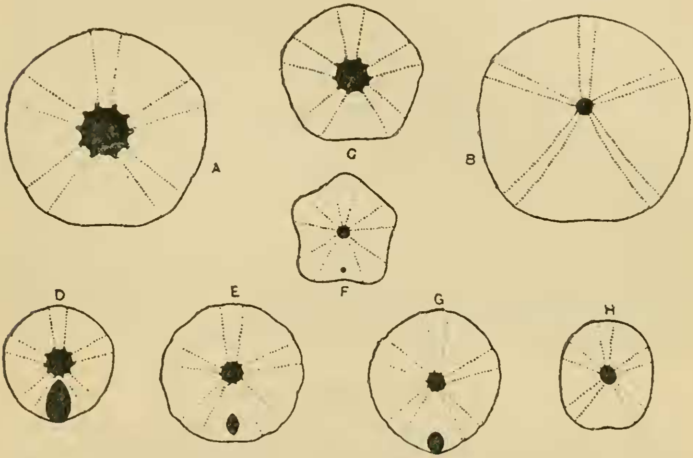
Among the *Pygasters*, when any departure from radial symmetry is encountered, it is found to result from a shortening of the antero-posterior diameter in proportion to the width of the test. This effect is appreciable in *P.* (*Megapygus*) *umbrella*, but reaches its extreme in *P.* (*Macropygus*) *truncatus*. It is in all probability due to an interference with the growth of the plates of the posterior interambulacrum by the great size of the periproct. The truncation of outline is rarely found outside the genus, but in *Desorella* and *Galeropygus* it reappears, often to an increased degree.

The slight groove which, in *P. semisulcatus*, passes from the periproct to the posterior margin, is probably due to the same cause as the shortening of the interradium. It is very interesting and suggestive to find a trace of the sulcus in this genus, in view of the fact that its presence is a notable feature in *Galeropygus*.

and most of the non-Holectypoid Jurassic Irregular genera. A further reference to this feature will be found in the section on the interambulacra (p. 465).

In *Holectypus* there is a tendency opposite to that of *Pygaster*, but one probably caused by the same agent. In such a form as *H. depressus*, where the periproct is of very large size and is situated on the adoral surface, there is frequently a backward projection of the posterior interambulacrum to accommodate it. Even with this projection, there is often but a thin rim of test between the periproct and the peristome—a fact which shows the necessity for some such arrangement. In many of the Jurassic species which have a marginal periproct, a similar tendency is seen (e. g., *Holectypus oblongus* Wright). Although the lengthening of

Text-fig. 54.



Diagrams of the adoral surface in some Holectypoida and their allies showing the shape of the ambitus and characters of the peristome.

A. *Pygaster semisulcatus*. B. *Galeropygus agariciformis*. C. *Pygaster* (*Macropygus*) *laganoides*. D. *Holectypus depressus*. E. *Discoidea cylindrica*. F. A Clypeastroid. G. *Conulus albogalerus*. H. A cretaceous Echinonoid.

the antero-posterior axis results in a bilateral symmetry comparable with that of many of the Echinoids which are more advanced in "Irregularity," it was not a feature retained by the Holectypoida after Jurassic times. All the species of the subgenus *Cœnholectypus*, and all of *Discoidea*, have an approximately circular outline. The slightly indented character of the interradii on the ambitus of *Discoidea* gives an alternating concavity and convexity to the margin which may be compared with that of a *Clypeaster*. In *Conulus* the tendency to elongation reappears, particularly in the large, high-zonal forms of *C. albogalerus*, where the marginal periproct is often situated on a considerable projection of the posterior interradius. The renewed appearance of bilateral symmetry under these conditions seems to confirm the belief that, so far as the Holectypoida are concerned, deviations from radial symmetry are connected with the migrations of the periproct, and depend upon them, having no real significance of their own.

2. *The Adapical Surface.*

With the exception of one rare form (*P. semisulcatus* var. *conoideus*), all the species of *Pygaster* are depressed. The conical shape is not quite regular owing to the interference of the periproct, and the apex is usually a little to the rear of the centre. In *Holectypus* the cone is rarely less elevated than in an average *Pygaster*, and is usually considerably higher. The extreme flatness of *Anorthopygus orbicularis* is quite exceptional for the group. The cylindrical form of *Discoidea cylindrica* is all the more curious because of the normally conical shape of the other and smaller species of the genus. The outline of *Conulus subrotundus* sometimes resembles it, but the vertical character of the sides is never so complete. The Upper Chalk *Conuli* tend, as a rule, to assume an acutely conical shape, so that the area of the adapical is sometimes twice as great as that of the adoral surface. The apex of the test is practically central in all the genera except *Pygaster*.

Among outside genera, almost the only forms to show the sharply conical shape of the Holectypoida are *Conoclypeus* and its allies. Most of the Clypeastroids are exceedingly flat in shape, while the bilaterally symmetrical groups naturally cannot be compared with the Holectypoida in this feature.

3. *The Adoral Surface.*

There is a very constant progressive change in the form of this region of the test within the group. From *Pygaster*, with a base so concave that specimens placed with the mouth downwards rest on the ambitus alone, to *Conulus*, where the base is to a considerable extent convex, every gradation may be traced. As this feature is directly associated with some of the peristomial characters, it will be better to postpone its discussion to that section of the paper.

B. The Peristome and Associated Structures.

1. *The Peristome.*

The central position of the peristome is constant throughout the group. In its size there is a progressive reduction traceable through the Jurassic to the Cretaceous forms. In *Pygaster* the peristome is of about the same size, relatively to the test diameter, as in an average Diademoid (about one fifth). In *Holectypus* a reduction is initiated, which is maintained and even accelerated in *Discoidea*, until in *D. cylindrica*, and also in *Conulus*, the peristome has only about one ninth the diameter of the test.

In dealing with this character it is important to realise that the size of the peristome is not of necessity directly connected with the presence or absence of jaws. It is true that in *Galeropygus* and *Pyrina*, where jaws were absent (at least, in adult forms), the peristome is quite small; but in the majority of the Clypeastroids the peristome is smaller in proportion than in these genera, and yet powerful jaws are present.

In the matter of the proportional representation of the ambulacral and interambulacral areas on the peristome margin, a slight but important change occurs in the course of the development of the group. In *Pygaster* sens. str., the proportions are 1 to 1·4 in favour of the interambulacra. In *Conulus* there is no appreciable difference in the share taken by the two areas. This change is partly due to the increased phyllodal tendency of the adoral parts of the ambulacra in *Conulus*, but still more to an actual narrowing of the interambulacra. In view of the extreme reduction which is found in the latter areas of *Clypeaster* and its allies, the progressive change, though slight, is significant.

Apart from the characters of the branchial slits, which will be considered in the next paragraph, the *shape* of the peristome undergoes no important changes until *Conulus* is reached. In that genus the circularity of its outline becomes slightly modified into an elliptical shape, with a tendency for the long axis of the ellipse to be oblique in its relation to the antero-posterior diameter. The departure from the circular form is very insignificant in itself, but when viewed in the light of the persistently elliptical, and usually oblique, peristome of the Echinoneidæ, it becomes invested with greater meaning.

2. *The Branchial Slits.*

All of the genera that I include among the Holectypoida possessed external branchiæ. Within the boundaries of the group, however, it is possible to trace the gradual reduction of these structures (as indicated by the shallowing of the peristomial slits through which they passed) until they become hardly appreciable in size. In no case are there signs of the smooth calcareous developments of the interambulacra, for the support of the gills in a recumbent position, which are characteristic of many of the Regularia Ectobranchiata. The slight modifications of the plate surface that exist are discussed in the section on the interambulacral areas.

In *Pygaster* sens. str., the branchial slits are extremely well marked (in *Megapygus* they are slightly shallower), and the depth of their incision renders the outline of the peristome festooned and decagonal. This stellate shape of the peristome is retained, though to a reduced degree, in *Holectypus*. In *Discoidea* the slits are so small that, in spite of the relative minuteness of the peristome, the margin is actually less notched than in *Pygaster*. In *Conulus* the slits are only just distinguishable on the thickened rim of the peristome. In *Pyrina*, and in the Echinoneidæ generally, they seem to be altogether absent.

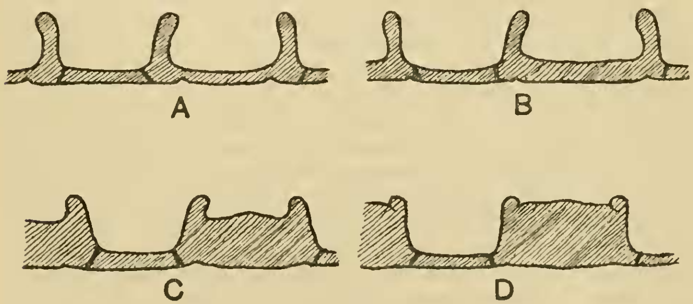
The concavity of the adoral surface is found to correspond fairly closely with the development of the branchiæ. In *Pygaster*, *Anorthopygus*, and *Holectypus*, the adoral surface is markedly concave, and the peristome is situated in an additional hollow in the centre. In *Discoidea* the surface is almost flat, and yet the peristome is deeply sunken. In *Conulus*, on the other hand, the mouth is practically flush with the test-surface. In the Regular Ectobranchiata the length and stoutness of the radioles are sufficient to keep the test permanently raised above the rock surface. The branchiæ are by this means kept free from the danger of becoming bruised or fouled by contact with the ground. In the Holectypoida the radioles were certainly not so strong as, and probably of far less length than, those of an average Regular Echinoid. As a consequence, the adoral surface would be usually very near to, if not in actual contact with, the rock surface. Such a condition would have a disastrous effect on such delicate organs as the external branchiæ. It seems possible, therefore, that the concavity of the adoral surface of the test is a device for sheltering these structures. In the case of *Discoidea*, where, for purposes of internal consolidation, the lower part of the test is flattened, the region of the peristome is sunk to a proportionately great degree to afford this shelter for the branchiæ. In *Conulus*, where the branchiæ were practically negligible in size, and probably in function also, no such precautions were necessary. For gnathostomatous forms, like the Holectypoida, which were presumably not wholly, or even chiefly, microphagous, this depression of the peristome would appear to be disadvantageous for the capture of food; and only the safety of the equally essential process of respiration could warrant such a development. However, it must be remembered in this connection that the Clypeastroids, in a considerable number of cases, possess a re-entrant peristome without any external branchiæ. They have grooves on the adoral surface converging on the mouth, which may counteract what seems to be an unprofitable structure. Moreover, among them the indentation of the peristome is in all probability connected with the accommodation of the large jaw-apparatus.

The Holectypoida offer no satisfactory evidence as to the relation between the peristomial and petaloid branchiæ. In the Upper Jurassic *Pygasters* (e. g., *P.* (*Megapygus*) *macrocyphus*) there is a marked tendency towards petaloid structure in the adapical parts of the ambulacra, but the branchial slits are as well developed as in any of the earlier species. As the genera are traced to the Upper Cretaceous, there is an irregular but frequent tendency seen for the adapical ambulacral pores to become dissimilar, but there is never any contrast sufficient to warrant a belief that ambulacral branchiæ were present. And so in *Conulus*, in the almost complete absence of peristomial gills, there seem to have been no special structures, either left or developed, to perform the function of respiration. In the Echinoneidæ the same condition obtains, but the Clypeastroida show an ever increasing perfection of adapical petals to compensate for the loss of the more primitive adoral branchiæ.

3. *The Perignathic Girdle.*

Detailed and valuable studies of this structure in *Discoidea* and *Conulus* have been made by Duncan and Sladen (**40** & **41**) and Lovén (**43** & **48**). These researches have the additional value that they were pursued with different aims. The former authors were intent upon demonstrating the absence of jaws in the two genera, while Lovén predicted, and later realised, their discovery in *Discoidea*. The structure of the perignathic girdles of *Pygaster* and *Holectypus* is not so fully known, and in the case of *Anorthopygus* there were no known traces of the girdle when Duncan (**44**) placed the genus in the same family with *Echinoneus*. Lovén (**48**) knew of its existence in all the three genera, but gave no details of its structure.

Text-fig. 55.



Diagrams of the perignathic girdles in

A. *Pygaster*. B. *Anorthopygus*. C. *Discoidea*. D. *Conulus*.

In *Pygaster* the processes are very strongly developed, while the ridges are hardly recognizable. There is no tendency for the processes to form an arch over the ambulacra—in fact, they slope away from one another. Thus there is initiated the persistently disjunct girdle which characterizes all the gnathostomatous Irregular Echinoids. In *Holectypus* the structure seems to have been practically the same, but there are indications that the ridges were slightly more pronounced. This was certainly the case in *Anorthopygus*. In *Discoidea* the processes are proportionately similar to those of *Pygaster*, but their prominence is almost masked by the extreme elevation of the ridges. In *Conulus* this latter feature is carried so far that, except for the suture-line showing that the process is present, the only visible and free portion of the ambulacral part of the girdle is a minute shining knob at each corner of the ridge.

It is, I think, a point of great interest to find that *both* ingredients of the perignathic girdle are so strongly developed in these later Holectypoid genera. One of the most obvious contrasts between the divisions of the Clypeastroids is the presence in some genera of one support for the jaws in each interradius, and in others of two. It would seem that, when they are double, these supports represent processes, and when single, they are the degenerate relics of ridges. Both such conditions could be obtained readily by the modification of a perignathic girdle in which both portions were equally represented. All that is necessary is a simple process of the elimination of one or the other of the parts.

Another feature of interest in the perignathic girdle of the Holectypoida, and one connected intimately with the method of use of the jaws, is the angle which the supports make with the plane of the adoral surface of the test. In *Pygaster* the processes are almost, though not quite, at right angles to that surface, with a slight outward slope. This inclination is rather more marked in *Anorthopygus*, and considerably so in *Holectypus*. In *Discoidea* the angle between the girdle and the floor of the test is quite acute, while in *Conulus* it becomes, especially in thin-tested forms, almost 45 degrees. The practically vertical girdle of *Pygaster* would indicate a correspondingly vertical working of the jaws, similar to that of the Regular Echinoids; while the highly inclined system in *Conulus* seems to show a tendency towards the horizontal working of the jaws of Clypeastroids.

In *Conoclypeus*, according to the description and drawings given by de Loriol (**35**), the two ambulacral processes are present, but the ridges have dwindled to insignificant proportions, both in width and height. This brings the processes closely together, and there is consequently induced a markedly Clypeastroid appearance in the perignathic girdle.

4. *The Jaws.*

Our knowledge of the jaws of the various genera of the Holectypoida is very meagre and unequal. In fact, of the details of the structure of the pyramids and teeth of Jurassic forms next to no evidence is at present available. There are two reasons why this condition of affairs should exist. Firstly, the jaws are internal organs, and so, if they are preserved in the interior of a specimen, it is necessary to break it up before they can be studied. Moreover, it is usual to find the matrix that filtered into the tests of Oolitic forms more compact and refractory in texture than the surrounding rock. Secondly, the large size of the peristome in the earlier genera would be liable to let the jaw-fragments slip through when their supporting muscles had decayed. As all the species of *Pygaster* and *Holectypus* are more or less conical in shape, the natural position that the test would assume when allowed to settle on the sea-floor would be with the oral surface downwards. After the jaws had slipped through the peristome they would, on account of their relatively light weight, become scattered by currents which were too gentle to move the whole test.

Jaws are known to exist in *Pygaster*, but I have been unable to find descriptions or specimens in which their structure was adequately shown. From the characters of casts of the pyramids preserved in an ironstone mould of *P. ? semisulcatus* that I have seen, these parts of the lantern seem to have been large and massive, and of a shape corresponding with that of the pyramids of *Cidaris*. Wright (**20**) has figured a specimen of *Holectypus depressus* in which the complete lantern is preserved. I have examined the specimen (B.M., E. 1687), but it is impossible to trace any of the ossicles to their extremities, so that no measurements of any value can be taken. The general facies of the pyramid is strikingly "Regular." Nothing seems to be known of the jaws of *Anorthopygus*, but they must certainly have existed.

For a long time the presence of jaws in *Discoidea* was doubted, and sometimes, notably by Duncan (**41** & **45**), absolutely denied. In 1892, Lovén, in the wonderful store of information as to the perignathic structures of Echinoids contained in his Echinologica (Lovén, **48**), gave a description of the pyramids in *D. cylindrica*, and recently I was able (Hawkins, **60**) to confirm and amplify his description with the additional features of the epiphyses and the teeth. In this genus the pyramids have still a markedly "Regular" appearance, although they were probably much more closely attached to the processes of the perignathic girdle than in any Regular Echinoid. This shortening of the muscles of attachment resulted in a far less vertical position for the lantern as a whole, while the strong incurving of the adoral parts of the pyramids will have increased the angle to one of about 45 degrees at the peristome. The teeth are curved considerably to correspond with this arrangement. They are strong, and built on the Echinoid plan, in contrast to the Diademoid, with a pronounced keel on the concave side.

In the case of *Conulus*, the long controversy as to the presence or absence of jaws has been partly settled by the discovery of teeth in a specimen of *C. subrotundus* (Hawkins, **65**). There is as yet no evidence as to the characters of the jaws; and the teeth in themselves, beyond their similarity to those of *Discoidea*, show no features of special interest. They are less curved than those of that genus, and more sharply pointed, the latter character being in contrast to what might be expected in view of the bluntness of Clypeastroid teeth. The peculiar structures in *C. albogalerus*, usually known as the "buccal plates," are probably in some way derived from jaw-ossicles, as their anomalous character separates them absolutely from the peristomial plates which exist in many other genera. In the paper to which reference has just been made, I have suggested a possible origin and function for the buccal plates, but it must be confessed that the theory advanced there has a very insecure foundation.

So far as is at present known, there is nothing in the structure of the lantern of the Holectypoida which even foreshadows the curiously expanded pyramids of the Clypeastroida. The probable delicacy of texture of the pyramids in *Conulus subrotundus* may indicate the incoming of a reticulate structure similar to that of the corresponding parts in *Clypeaster*. With regard to the manner of working, the angle of setting of the jaws shows a progressive tendency towards the Clypeastroid method. This retention of the "Regular" facies of jaw-structure throughout the group is rendered the more remarkable by a comparison with the fragmentary pyramids in *Conoclypeus* described by de Loriol (**35**). That genus, with its Clypeastroid (almost Echinanthine) general build, seems to have possessed the compact pyramids of a *Discoidea*. It is true that the only record of its jaws is very imperfect, but this much seems obvious on a study of de Loriol's drawings. But in *Conoclypeus*, in spite of the Holectypoid jaw-structure, the perignathic girdle is very like that of *Clypeaster*.

The recently described teeth and lantern in a young specimen of an *Echinoneus* (Agassiz, **58**) have a most important bearing on the relation between the Holectypoida and the Echinoneidæ. The presence of the jaws is undoubtedly a vestigial character, for they seem to be resorbed while the individual is still quite immature. The jaws and teeth both have a *Discoidea*-like appearance, rather than a *Clypeaster*-facies. It is probable that, as they exist in the young stages of *Echinoneus* (the most advanced member of its family), they will have been present in such genera as *Pyrina* at a corresponding stage of development. The likelihood of their discovery in fossil forms is extremely remote, owing to their minute size and delicate texture, but analogy tells strongly in favour of their existence. This discovery is a remarkable instance of the completion by Ontogeny of an unfinished chain of evidence supplied by Palæontology, and removes any doubt which may have existed as to the intimate relationship which links the Conulidæ with the early Echinoneidæ.

In this connection it seems well to suggest the possibility that Lovén's genus *Pygastrides* (Lovén, **43**), a "*Pygaster*" lingering so long after the day of the Holectypoida was past, may be only another example of the vestigial gnathostomatous stage of some, probably Echinoneid, genus. So strongly am I of this opinion, that I have omitted its name from the new classification.

C. The Periproct.

Since the excentric position of the periproct, outside the apical cycles of plates, is a diagnostic feature of the Irregular Echinoids as a whole, it is natural to find that in the Holectypoida, which includes the most primitive of the "Exocyclic" forms, its position is very variable. When once the periproct has left the apex, its chief tendency seems to be to assume a position as absolutely posterior as possible, and in the course of its passage to such a position, it undergoes many changes itself, and is the cause of many others to the test. It always lies in the posterior interambulacrum.

1. *The Position of the Periproct.*

Practically the only distinguishing feature between a young specimen of a *Pygaster* sens. str. and a primitive Diademoid is the fact that in the former the periproct has broken through the posterior part of the apical system. It cannot be said to lie altogether *outside* the system, for to some extent it occupies the position of the posterior genital plate, and extends well up to the apex of the test. It is, in part, more nearly central in position than in some of the Saleniidæ, although its large size causes it to reach away from, as well as into, the apical system.

In *Pygaster* sens. lat., the periproct is always in contact with the apical system,—in the earliest forms reaching to the inner margins of the anterior and antero-lateral genitals, and in the later ones touching only the outer margins of the redeveloped posterior genital. When traced from *Pygaster* sens. str. to *Macropygus*, however, the position of the widest part of the periproct is found to pass gradually backwards, while the posterior edge of the opening approaches the ambitus of the test. *Pygaster*, then, shows a stage in which, although the periproct retains its primitive association with the apical system, the posterior tendency in its position is recognizable.

Pileus and *Anorthopygus* agree in having the periproct entirely on the adapical surface of the test, but quite separated from the apical system. In most cases, however, the posterior part of the periproct is not so near to the ambitus as in *Macropygus*.

In *Holectypus* we find two groups, as regards the position of the periproct. Both groups appear at almost the same stage of the Lower Oolite, but one is more retarded in character than the other. The former, which may be exemplified by *H. hemisphæricus*, has the periproct opening on the margin, that is, in the posterior extremity, of the test. The latter, of which a common representative is *H. depressus*, has the periproct entirely on the adoral surface, and often very close to the peristome. It would appear at first sight that in the former group the periproct had reached the necessary limits of its retrogression, and in the latter had, as it were, overshot the mark. But, in the light of the later genera, it is impossible to regard the adorally situated periproct of *H. depressus* as a case of overspecialization. Most of the species of *Cœnholectypus* have the periproct in that position, as have all the forms of *Discoidea*. The *H. hemisphæricus* character reappears in *Conulus*, and is retained in most of the Cretaceous species of *Pyrina*.

Text-fig. 56.

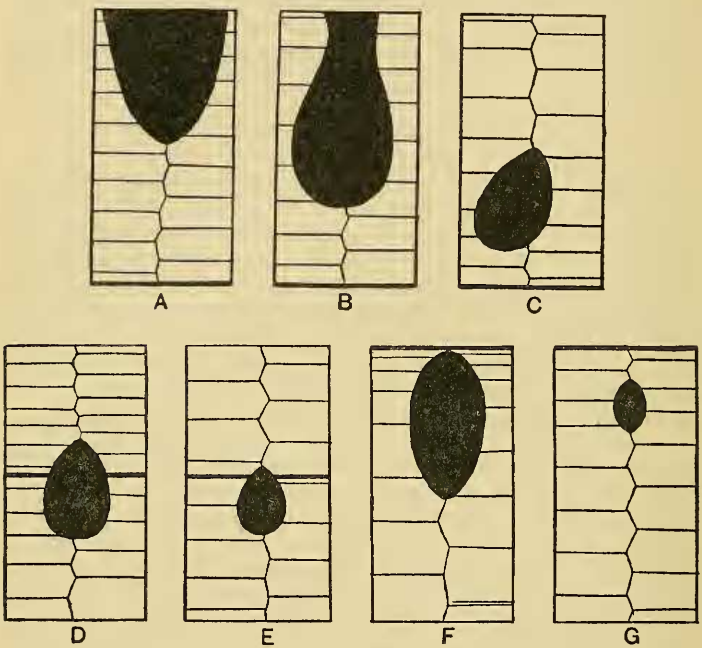


Diagram showing the shape and position of the periproct in A. *Pygaster* sens. str., B. *Megapygus* or *Macropygus*; C. *Anorthopygus*; D. *Holectypus* (*hemisphæricus*); E. *Conulus*; F. *Holectypus* (*depressus*); G. *Discoidea*. The thick line represents the ambitus. The proportionate height of the interradial plates is indicated.

Lovén (**36**) has indicated the correspondence in periproct-migration that exists between the Holectypoida (his Echinoconidæ) and both the Echinoneidæ and Cassidulidæ. *Galeropygus* and *Clypeus* both have the *Pygaster*-like periproct, in contact with the apical system, while the Nucleolitidæ show an arrangement more like that of *Pileus*. The Echinolampidæ include forms in which the periproct may be marginal or adoral in position.

In connection with the position of the periproct, an interesting feature of the posterior interradius may be discussed. Reference has been made already (p. 455) to the truncated form of many of the *Pygasters*, and of *Galeropygus*, and the comparatively elongated outline of some *Holectypi* and of *Conulus*. The truncation of the posterior interambulacrum is associated with the presence of a more or less defined posterior sulcus; and, in fact, whenever the periproct is on the adapical surface, this sulcus is developed. The functional value of a sulcus below the anus is obvious, as it would tend to restrict the passage of fæcal matter to a definite channel, and so to prevent it from coming in contact with the podia. But the developmental meaning of the structure would seem to concern the interference in the growth of the interambulacral plates by the periproct. These plates, formed at the apex and forced downwards towards the ambitus, have to separate along their median sutures to pass round the periproct, and subsequently have to close together below it. The irregularity thus caused results in a retardation of their downward movement (and a consequent shortening of the distance from the apex to the posterior margin of the test), and in a sagging inwards of the reconstructed portions of the plates to form a groove. The probability of this explanation of the structure so characteristic of *Pygaster*, *Galeropygus*, and the Nucleolitidæ, becomes increased when the opposite conditions are considered. When the periproct is marginal or inframarginal in position, the interambulacral plates can pass freely over the adapical surface until the edge of the periproct is reached. Here, in consequence of the lessened width of the divided halves of the area at the sides of the periproct, a delay in the progress of the plates occurs. As a result, the oncoming plates become heaped up against one another above the periproct, and give rise to the elongated, carinate posterior shape which characterizes *Holectypus* sens. str., *Conulus*, and also the Spatangoida.

Although it must be admitted that the two opposite conditions, sulcate and carinate, of the posterior interradius have, from a teleological standpoint, an obvious and similar functional value, the explanation given above seems natural in view of their regular association with the position of the periproct. In the case of the Spatangoida, there is the complication of a "posterior surface" to the test, at the upper part of which the periproct is situated. If this surface were curved in conformity with the rest of the test, the periproct would open at a point about midway between the apex and the ambitus, as in *Pileus* or *Anorthopygus*. It seems to me to be a very striking fact that, in the last-named genus, no trace of a posterior sulcus is developed, but that the declivity of the test is appreciably increased *as a whole* in the region behind the periproct. The Spatangoid posterior surface might, then, be regarded as the product of a retarded growth of the entire posterior interambulacrum owing to the interference of the periproct, while the carina above it would be caused by the same agent in its opposite influence.

In the few cases where absolute circularity of outline is regained in the Irregular Echinoids, as in *Discoidea* and many Clypeastroida, the periproct is so small as to necessitate very little modification of the steady progress of the coronal plates from the apex to the peristome.

2. *The Shape of the Periproct.*

In *Pygaster* sens. str., the periproct is roughly elliptical in shape, and very large, often having the same width (in transverse measurement) as the apical system. In *Megapygus* and *Macropygus* its outline becomes pyriform, owing to the partial closing in of the interambulacral plates round its adapical extremity. The width never becomes greater than in *Pygaster* sens. str., but the actual size is much larger in these later subgenera, owing to the backward shifting of the posterior edge of the periproct without a corresponding retraction of the adapical margin. The pyriform shape caused by this lagging behind of the upper part of the periproct leaves its impression on the shape of the aperture in later genera. In *Holectypus*, for example, the periproct has its adoral margin rounded, but adapically it tapers to a point. The same feature is seen in *Pileus*. In *Holectypus* sens. str., the periproct is still large; in some species, e. g., *H. depressus*, it is of an extraordinary size. But in *Cœnholectypus* it has generally decreased so as to be smaller than the peristome. In *Anorthopygus* the periproct is of moderate size, and has a characteristically oblique position. Obliquity in the case of the peristome is not uncommon among Irregular Echinoids (e. g., *Pyrina* and *Trematopygus*), but this is practically the only form where such asymmetry affects the shape of the periproct to a considerable degree. In this connection it is interesting to find that in *P.* (*Megapygus*) *umbrella* the large pyriform periproct shows a distinct inclination towards the left side of the interradius, thus giving an indication of potential obliquity.

In *Discoidea* the periproct is usually lanceolate in outline, often equally pointed at both extremities, but it is always longer than broad. In *Conulus* the marginal periproct is similar in shape to that of *Holectypus hemisphæricus*, although smaller in size. The pointed character of its adapical part is more pronounced in young specimens than in adults. The size and shape of the periproct in the Echinoneidæ compares well with those in the Conulidæ. In the Clypeastroida the periproct is always adorally situated, as in *Discoidea*, but it is very small, and usually circular in shape.

3. *The Anal Plates.*

The plating of the periproct-membrane is at present unknown in *Pygaster*, *Pileus*, and *Conulus*. In the case of the two genera first named, this is probably due to the large size of the periproct, and the resulting flexibility of the membrane and weakness of the plating. In the case of *Conulus* (and also of those *Holectypi* which have the periproct marginal), the exposed position of the anal plates on the ambitus may account for their non-preservation. A thickly plated membrane occupies the periproct of *Echinoneus*.

In *Discoidea* the plates of the periproct are not infrequently found *in situ*, and they are known in *Cœnholectypus*, *Anorthopygus*, and *Coptodiscus*. The last-named genus differs, as regards this character, from all the others, in possessing a single ring of almost equal-sized plates around the inner margin of the periproct, and in not having, so far as is known, any smaller plates in the immediate surroundings of the anus.

Discoidea has one large anal plate, usually bearing a tubercle, occupying most of the adoral half of the periproct-opening, and a series of fringing plates which decrease in size as they approach the adapical part of the aperture. A few, often only two, small plates occur within this irregular ring, and they are always in contact with the largest plate. The anus is thus situated quite near to the adambital edge of the periproct, in a position far removed from the mouth. In *Cœnholectypus*, to judge by a figure of *C. jullieni* from Algiers (Péron & Gauthier, **34**), the arrangement was on a similar plan. There, however, the adorally situated plate is relatively small, and the fringing plates are also smaller and more numerous than in *Discoidea*. The inner anal plates are exceedingly minute, and are preserved in considerable numbers.

In *Anorthopygus* I have been able to study only the outlines of the anal plates, these being easily traceable on a siliceous mould of *A. orbicularis* in the British Museum. In this specimen the arrangement of the plating is exactly the reverse of that which obtains in the two genera just described. The largest of the anal plates are adapically situated in the oblique periproct, and a series of pentagonal and hexagonal plates, of approximately equal size, covers all the remaining surface of the aperture except for a very small area in its extreme adoral part. The actual anus, which is represented in the mould by a prominent unsutured portion of the infilling matrix, lies in the true antero-posterior axis of the test, thus being unaffected by the asymmetry of the periproct as a whole. There seems to have been no space occupied by plates between the anus and the periproct margin.

The position of the anus, in its relation to the situation of the periproct on the test, is interesting. When the aperture is on the adoral surface the anus tends to open in its adambital corner, while the same tendency, with an opposite effect, appears when the periproct is supramarginal. A generalization, founded on the somewhat slender evidence of only three generic types, may be made that:—Wherever the periproct may be situated, the anus assumes a position within its borders as near to the ambitus (*i.e.*, the most posterior part of the test) as possible.

D. The Ambulacra.

1. *The Podial Pores.*

Although one of the diagnostic characters of the Holectypoida consists in the apetaloid nature of the ambulacra, it would be a mistake to assume that the pore-pairs are therefore similar throughout the group. The Nucleolitidæ, which are a group of almost the same antiquity as the Holectypoida, early developed a marked heteromorphy in the podial pores of the adapical surface; and a similar character, continually recurring, but as often held in check, is apparent among all the Jurassic members of the order. *Pygaster* sens. lat., has uniformly larger pores on the adapical than on the adoral surface, and the members of an individual pore-pair are dissimilar in the former region of the test. Even *Pygaster semisulcatus* sometimes shows this feature. The outer pore of the pair is a little larger than the inner, although both are somewhat elliptical in shape. In *P.* (*Megapygus*) *umbrella*, and still more in *M. macrocyphus*, the difference becomes increased. The inner pore is circular, and the outer retains an elliptical shape, often on quite an elongated plan. The long diameter of the outer, elliptical pore never becomes more than twice as great as the diameter of the inner, circular one; so that the whole ambulacrum cannot be said to show even a subpetaloid structure. In *Pygaster*, while this dimorphism of the adapical pore-pairs increases, the size of the pores on the adoral surface steadily decreases. These latter pores are always circular, and the members of each pore-pair are separated by a prominent granule. Their small size renders them quite difficult to distinguish in the Upper Jurassic forms.

In *Holectypus* a similar tendency is seen, although it is hardly appreciable in the Cretaceous subgenus. The diversity of shape and size in the adapical pore-pairs is rarely carried so far as in *Pygaster*, but the reduction in the diameter of the ambital and adoral pores is quite as well marked. In the case of *Discoidea* the tendency is less noticeable. The pores of the adapical surface are only very slightly larger than those of the adoral (both series being minute), and are themselves always circular. The outer member of a pore-pair is sometimes just distinguishable from the inner one in point of size.

In *Conulus*, by way of contrast, the pores of the ambulacra are everywhere exceedingly minute, those of the adapical surface being even smaller than those of the adoral. The largest pores in this genus are generally situated on or near the ambitus.

Discoidea, and to a further extent *Conulus*, may be regarded as illustrating the triumph of simplicity of ambulacral structure over the persistent tendency to complexity which induced variation in the earlier genera. In the case of *Discoidea*, the simplicity would seem to have been short-lived as soon as its successor, *Conoclypeus*, had emerged from the order Holectypoida, and initiated the Clypeastroida, where often the petals are developed to a great degree. As regards *Conulus*, only the Echinoneidæ, among its external relatives, retained the apetaloid character. The Echinolampidæ and the *Conulopsis* group show a pronounced subpetaloid development. Nevertheless, the fact remains that, in the matter of their ambulacral pore-structure, the later genera of the order conform more absolutely to the letter of the diagnosis than the earlier forms.

Text-fig. 57.

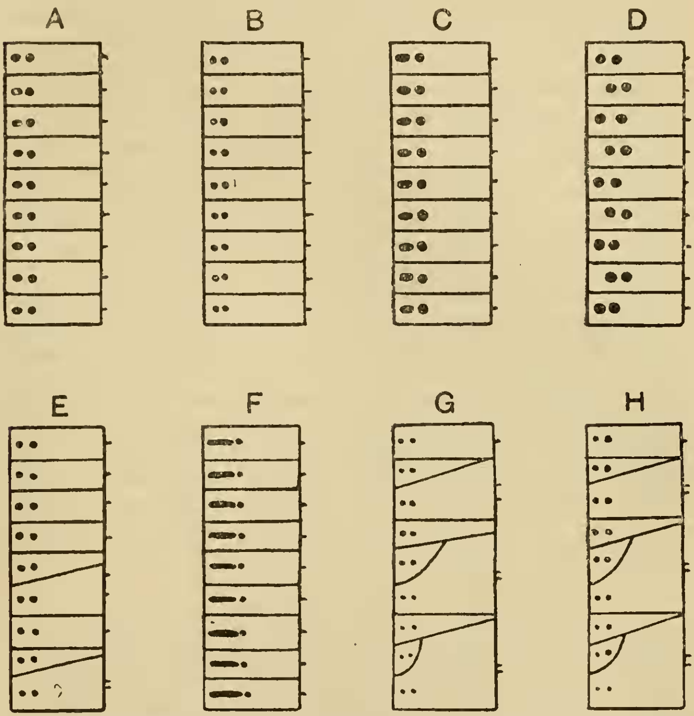


Diagram showing some characteristic plates of the ambulacra (from the adapical surface) in A. *Pygaster* sens. str.; B. *Galeropygus*; C. *Megapygus*; D. *Pileus*; E. *Discoidea*; F. *Conoclypeus*; G. *Conulus*; H. *Pyrina*.

The pore-pairs in *Pileus* show an anomalous character in being biserial on the adapical surface, without any corresponding interference with the primary nature of the ambulacral plates. There seems nothing among Irregular Echinoids to compare with such a condition, which recalls the similarly inverted development of biserial pore-pairs in the ambulacra of *Diplopodia*. The somewhat analogous appearance of the pores in the anterior ambulacrum of the Spatangoid *Heteraster* is accompanied by "plate-crushing" in the structure of the area. *Pileus*, in this respect, as in some others, must be regarded as a curiously specialized offshoot from the *Pygaster*-stock, which only survived a short time, and left no descendants.

2. *The Ambulacral Plates.*

Recently, in the 'Geological Magazine' (Hawkins, **62**), I indicated in outline the principles of ambulacral structure which characterize the Holectypoida. Later (**66**) I extended the line of enquiry to the other Jurassic groups of Irregular Echinoids, and showed the influence that plate-structure exerts on the features of the phyllode. It will, therefore, be necessary only to summarize the results of those studies here, for the sake of completeness.

All the Holectypoida show a crushing together of the primaries to form compound plates in their ambulacra. The degree of crushing is a progressive one. Most of the ambulacrum of a *Pygaster* is composed of primaries, while hardly any unmodified primaries remain in the ambulacrum of a *Conulus*. The building of the compound plates is carried out on a perfectly uniform plan, three original plates going to form one compound plate. The significance of this triple arrangement will be discussed at the beginning of section V. of this paper. *Conulus* differs from all the other genera of the order (except the little-known *Discoholectypus*), partly in the early stage at which the crushing commences, and partly in the fact that two out of the three plates concerned retain their primary character (though modified in shape) for a considerable distance beyond the first crushing point, often right down to the ambitus. Two genera may be cited, representing two widely divergent groups, which show an exactly similar ambulacral structure. These are *Pyrina*, of the Echinoneidæ, and *Amblypygus*, of the Echinolampidæ. It is hard to believe that so peculiar a structure can have been evolved four times independently.

Although there is no true phyllode-structure (nor appearance) developed in the adoral parts of the ambulacra in any of the Holectypoida, the nature of their plate-crushing inevitably results in a "hypophyllodal" character (see Hawkins, **66**) of that region. It is not until *Conulus* is reached, however, that the displacement of the plates drives the pore-pairs into a definitely triserial order. In *Pygaster* the pores hardly deviate from a straight line throughout the length of the ambulacrum, and no regular displacement can be traced in the poriferous zones of *Holectypus*. In *Discoidea* the pore-pairs become appreciably triserial midway between the ambitus and the peristome, but recover their linear arrangement before the peristome is reached. In *Conulus* a triserial character appears practically at the ambitus, and becomes more pronounced as the ambulacrum is traced towards the mouth; until, near the peristome, the triads are inclined at an angle of 45 degrees to the direction of the radius.

The greatest difficulty that appears when an attempt is made to trace a phylogenetic sequence from the Holectypoida to the

Clypeastroida is the presence in the latter group of a few large ambulacrals in the adoral parts of the area, with no signs of plate-crushing. Can a compound plate be resolved by evolution into its constituent primaries, or is the simplicity of the Clypeastroid ambulacral only apparent, being in reality the result of the fusion of the components of a compound plate, followed by the atrophy of two of the three pore-pairs? Bather (59) has expressed his belief in the possibility of the former process in his discussion of the ambulacrals of *Orthopsis*. In support of the alternate suggestion it may be remarked that in the Clypeastroids the pore-pair of each large polygonal ambulacral is situated near the adoral margin of the plate, leaving a high non-poriferous region along the rest of the adradial margin. Moreover, in the case of *Discoidea* just cited, the triserial arrangement of the pore-pairs is arrested soon after its inception, and the poriferous zones again become straight. There seems to be no indication of a corresponding reduction in the degree of compression of the demi-plates towards the peristome, but rather an increase, until the platelets become so minute that the small pore-pair can hardly find room to pass through the test within its borders. The presence of this feature of simplification in the sequence of the pores, but not in the structure of the ambulacral plating, in *Discoidea* seems especially significant; for *Discoidea* is the nearest ally of the Clypeastroids that is found among the Holectypoida. However, I do not feel justified in expressing a positive opinion, in one or the other direction, upon this question. Much must be done in the study of the postlarval growth of the test in the Clypeastroids before any proof of the origin of their ambulacral structure can be expected.

E. The Interambulacra.

1. *The Interambulacral Plates.*

The interambulacral are always much broader than the ambulacral areas, and the proportionate width (about 3 : 1 at the ambitus) is retained almost unchanged from *Pygaster* to *Conulus*. Owing to the absence of expanded petals and phyllodes in the ambulacra, there is no compression of the adapical or adoral extremities of the interambulacra such as occurs in most of the Irregular Echinoids. The areas increase regularly in width from the margins of the genital plates to the ambitus, and decrease as regularly, though more rapidly, from the ambitus to the peristome.

In *Holectypus depressus* there are shallow pits on the transverse sutures at points directly above the branchial slits. I know of no evidence which could ascribe a function to such features. The interradial suture is usually only slightly zigzag in character, and in some forms, notably among the Jurassic *Holectypi*, it is practically straight, so that the plates become roughly rectangular in outline instead of being pentagonal. The plates of the adapical surface are generally much broader than high, but on the adoral surface this difference is lessened. In *Holectypus* sens. str., the contrast in the height of the plates of the two surfaces results in the presence of very few interambulacrals on the adoral surface. In *Pygaster* the difference is not so strongly marked.

The only member of the group in which any striking difference in the appearance of the interambulacral plates themselves occurs is the peculiar genus *Coptodiscus*. Here, in a form otherwise hardly to be distinguished from *Cœnholectypus*, all the margins of the plates are bevelled, so as to leave deep grooves along the sutures. This feature, which recalls the similar structures in *Goniocidaris* and the Temnopleuridæ, is restricted to the adapical surface. Whether it is a result, in this case, of a paucity of carbonate of lime in the water, or of some physiological peculiarity, it is impossible to judge. The feature seems to be quite unique among the Irregular Echinoids.

2. *The Primary Tubercles.*

In their structure and proportions, the primary tubercles show no more variety, when traced through the group, than do the radioles that they support. The equality in size of those of the adapical and adoral surfaces, which is marked in *Pygaster*, becomes gradually replaced by a tendency towards an increase in size of the adoral tubercles, with a corresponding decrease of those of the adapical surface. In *Discoidea*, especially in *D. subuculus*, the reduction of the adapical tubercles has proceeded so far that they can hardly be distinguished in size from their attendant miliaries. Apart from a tendency in *Conulus* for the boss to become wholly convex in side view, and so fill the scrobicule more completely than do the partly concave sides of the boss in *Pygaster*, there are no changes of importance to be traced in the actual structure of the tubercles.

In the arrangement of the tuberculation more variation is found, and there becomes manifest a continual tendency towards a progressive increase in its complexity. I have dealt with this character (Hawkins, **67**) in considerable detail, and give here a summary of the results obtained in my recent paper.

As Saemann and Dollfuss (**27**) showed, the actual number of tubercles present on each interambulacral plate depends largely on the size, that is, on the age, of the individual. In all the Holectypoida there is at least one plate, at each end of the half interradius, which supports a single tubercle. This is obviously a relic of the primitive, unituberculate character of the plates of the earlier Regular Echinoids. The number of such plates remaining decreases steadily as the group is traced from the Lower Jurassic to the Upper Cretaceous. The median series of tubercles persists in an unbroken line from the apex to the peristome, but, except in *Pygaster*, is not readily distinguishable from its associates in point of size. Each tubercle in this median series is placed slightly nearer the adoral than the adapical transverse margin of the plate. All the other tubercles, of which

Text-fig. 58.

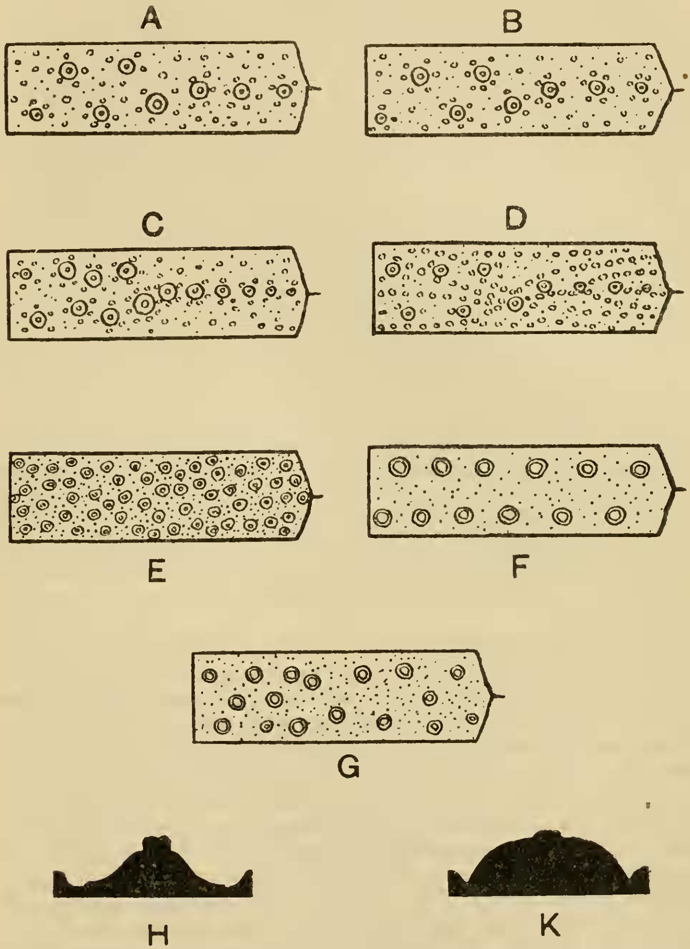


Diagram showing the third plate above the ambitus in A. *Pygaster* sens. str.; B. *Holectypus (hemisphæricus)*; C. *Holectypus (depressus)*; D. *Discoidea*; E. *Galeropygus*; F. *Anorthopygus*; G. *Conulus*. Figs. H & K are side views of primary tubercles in *Pygaster* and *Conulus* respectively.

great numbers may occur in the later genera, are developed in recognizably vertical series. When their number becomes great, a natural tendency to slight irregularity appears, but this is never sufficient to mask the plan of the tuberculation. Irregularity generally consists of either the suppression of a member of a series on one plate (a feature often seen, even in the primary row, in *Echinus*), or its replacement by two tubercles. The Holectypoida are peculiar among Irregular Echinoids in retaining throughout life the unituberculate plates and the vertical arrangement of the tubercles. Only the Echinoneidæ show any similar plan, and in them it is very much obscured by irregularity of development. Some forms of *Pygurus* (e.g., *P. blumenbachi*) have one or more unituberculate plates at the adapical extremities of their interambulacra, but this retardation of development is obviously due to the considerable narrowing of the plates caused by the expansion of the ambulacral petals. However, most, if not all, of the Irregular Echinoids whose post-larval development has been studied, show a unituberculate stage. This is notably the case in *Echinolampas* (see Agassiz, **30**).

The tubercles of the additional series which develop on the interradial tracts are at first situated each in the middle line (in a vertical sense) of the plates. This results in a transverse line of tubercles extending between the main series and the interradial suture. The concentric arrangement thus caused characterizes *Pygaster* sens. lat., *Holectypus* sens. lat., and *Discoidea*. It seems somewhat irregular in the case of *Pileus*, and is definitely absent in *Anorthopygus* and *Conulus*. In these two genera the tubercle series of the interradial tracts appear near to the adapical and adoral margins of the plates alternately, thus giving an oblique arrangement (sloping interradially and adorally) to the tubercles in the complete interambulacrum. A similar arrangement to this affects the adradial tubercle-series in all the genera of the group.

The oblique setting of the tubercles results in a much more uniform and packed tuberculation over the whole area than exists when the interradial series are transverse. The closeness of the arrangement is increased by the doubling of many of the tubercles in *Conulus*; so that, instead of two tubercles, three or even four are concerned in the composition of the oblique line on each plate. The complexity of arrangement, coupled with a homogeneity of character, of the tubercles, which was thus slowly obtained during the course of evolution of the Holectypoida, was rapidly developed, and carried to a further degree, by the earliest of the non-Holectypoid Echinoids. The species of *Galeropygus* from the Lias show typically the bewildering profusion of small tubercles which characterize the interambulacra of all the Nucleolitidæ, "Cassidulidæ," Clypeastroida, and early Spatangidæ. Only the Echinoneidæ seem to preserve a *Conulus*-character in their tuberculation, and in them it becomes so irregular as to be hardly appreciable except in the newest formed plates.

The peculiar sunken supernumerary tubercle of some of the adapical interambulacrals of *Holectypus depressus* from the Cornbrash recently described (Hawkins, **67**) is without a parallel among the other members of the order. Although suggesting a comparison with the large interpetalous interambulacral tubercles of such a genus as *Eupatagus*, it seems to be a specific character of no genetic value.

3. *The Miliary Granules.*

In *Pygaster*, and to a less degree in *Holectypus*, the granulation shows a "Regular" affinity in being grouped around the primary tubercles to form scrobicular rings. This circular arrangement is not retained after the Jurassic period. In *Holectypus*, especially in *H. depressus*, the scrobicular miliaries on the adradial tracts of the plates near the peristome are often guttate in form. In *Macropygus* and *Anorthopygus* the large size of the scrobicules of the primary tubercles leaves little room for miliaries, but those which exist do not appreciably group themselves around the primaries. In *Discoidea* and *Cœnholectypus*, and to a slight degree in *Holectypus* sens. str., rows of granules radiate from the central primary tubercle, maintaining a more or less transverse direction, to reach the adradial and interradial margins of the plate. In the genus first named these linear rows of granules become interspersed, near the ambitus, with additional tubercles.

In *Conulus* the granulation is apparently without a definite system of arrangement. The granules are sunk slightly below the level of the test on the adapical surface, being enclosed in minute pits. On the adoral surface they regain their projecting character, and often occupy broad bands, slightly elevated, which correspond in position with the transverse sutures of the plates.

F. The Radioles.

Our knowledge of the acanthology of the Holectypoids is fragmentary and inadequate. Enough is known, however, to show that there exists a considerable uniformity in the character of the radioles throughout the group. Wright (**20**) has described the primary radioles of *Pygaster*, in the species *semisulcatus* and (*Macropygus*) *morrisii*. For both he uses almost the same words—short, needle-shaped bodies with fine longitudinal lines on the stem. I have not seen any specimens in which they are preserved. In the case of *Holectypus* there is a specimen of *H. depressus* (from the Inferior Oolite of Cheltenham) in my collection which retains a considerable number of radioles on both the adapical and adoral surfaces. Wright (*t. c.*) describes them in the same species. The primaries of the upper surface are very short and slender, with blunt tips. Those of the adoral surface were apparently quite long, and but slightly tapering. The collars of the adoral radioles are prominent, and often very oblique. The shafts of both sets of radioles are longitudinally fluted with closely-set ribs. The miliary granules support spines of a similar character to the adoral primaries, but far more minute, so that Wright's description of them as "hair-like" is accurate.

I have been unable to find any record of the preservation of radioles in *Discoidea*. In *Conulus* the primaries are very much like those of the adoral surface of *Holectypus* in shape and ornament. The miliaries support curiously blunt prominences, which are usually preserved *in situ*, but are very easily rubbed off by too vigorous development of the specimen. These blunt spines were figured by Forbes (**14**), who also gave a drawing of a curious body that he regarded as a pedicellaria. The characters of the miliary spines suggest a comparison with the calcareous supports of pedicellariæ; but if they all had this function, the number of those organs would be extraordinarily great in proportion to the radioles.

Nothing seems to be known as yet of the microstructure of the radioles of any genera of the group, as Hesse (**51**) did not choose an Holectypoid for his researches.

The slight progressive change traceable in the primary radioles seems to lead merely to an increase in the length, and perhaps in the slenderness, of their shafts; while, as would be expected from the difference in size of the tubercles on the two surfaces of the test, the adoral radioles become proportionately longer than those of the adapical surface.

G. Internal Buttresses.

The difference in form which makes so violent a contrast between a *Scutella* and an *Echinus* must result in a corresponding difference of resisting power against the pressure of the waves. As both types of Echinoid may live between tide-marks, where the violence of the waves is most felt, they both have the same forces to repel. A spherical body such as that of an *Echinus*, or even a hemispherical one, like that of an *Holectypus*, could easily ward off the blow of a breaking wave, in the same manner as a *Patella* does. But a flat test, such as that of a Scutellid, would offer a blank resistance to the waves, and, if hollow, would almost certainly be crushed. For this reason, the few groups of the Irregular Echinoids that frequent the exposed littoral habitat so characteristically occupied by the Regular forms, strengthen the resisting power of their tests by the development of massive calcareous buttresses within. Practically the only Irregular forms which live openly on the shore at the present day are the Clypeastroida. It becomes, therefore, a point of especial interest to find the beginnings of internal supports to the test among the Holectypoida, which is the only other gnathostomatous (and therefore rock-dwelling) order. Although the development of the buttresses in the two groups might easily be regarded as an illustration of similar adaptation to similar environment alone, yet, in the light of the other less obviously utilitarian features of the two groups, it seems in this case that a genetic explanation exists as well.

On the internal mould of a *Pygaster*, and yet more in one of a *Pileus*, besides the deep pits left by the prominences of the perignathic girdle on the adoral surface, there are grooves (representing ridges in the test) that pass from the processes alongside the ambulacra (but situated on the interambulacra) for a short distance. The structure might be regarded as indicating a gradual rise of the inner surface of the test to form a keel which culminates in the perignathic process. As, among Regular Echinoids, the perignathic girdle rises quite abruptly from the inner surface, this gradual rise of the test towards the processes shows a new feature, the beginning of the inner buttressing of the test.

In *Holectypus*, as the name implies, a diagnostic feature of the genus as first tentatively suggested by Desor (**11**) is the absence of grooves in the internal moulds. This of course means the absence of internal ridges passing radially outwards to a point beyond the ambitus. An investigation of some siliceous moulds of *H. ? sarthacensis* has shown me that, although there is nothing in the interambulacra to compare with the strong "*cloisons*" of the succeeding genus, there nevertheless exists a considerable thickening of the adoral regions of those areas, even more than in *Pygaster*. In *Discoidea* the first signs of a really efficient internal buttressing appear. Down a line, rather to the adradial side of each half-interradius, there passes a thickening of the test which is rounded near the peristome and becomes carinate further out, and which extends beyond the ambitus. The partitions do not pass for any considerable distance up the adapical surface. The perignathic girdle tends to lean against the adoral ends of the supports.

In *Conulus* no such well-marked buttresses appear, but the interambulacral areas undergo a great amount of thickening towards the peristome. Indeed, the perignathic girdle, which is itself well developed, is often less internally elevated than the interambulacral plates against which it reclines. The ambulacra pass in sunken grooves across the adoral surface. In one specimen, on cutting a section through the interambulacrum at a point just outside the perignathic girdle, I found a large hollow to be included between an inner and an outer wall of calcite. I have not been able to verify the occurrence of this feature in other sections. It may, therefore, have been an abnormality or the result of an accident; but if it should be found to be a general tendency, or even one of fairly frequent occurrence, it would be very significant in the comparisons that might be drawn between it and the double flooring of the test of many of the higher Clypeastroida.

It is only in *Discoidea* that the buttresses are in such a freely projecting condition that they could be expected, by a growth in their height and an accompanying depression of the adapical surface, to form complete vertical partitions in the test. As it is, these "*cloisons*" of *Discoidea* are rather more strongly developed than the corresponding structures of *Echinocyamus*, which otherwise they resemble very closely. In fact, Gregory (**50**), in renaming the "genus" called *Echinites* by Duncan (**44**), which included only the species *Discoidea subucula*, used the name *Protocyamus* "to indicate the affinity of this Echinoid with the *Echinocyamus* series." The name, on systematic grounds, must be abandoned, but its significance remains.

In *Conulus*, but, so far as I am aware, in that genus only, a definite "sand-canal," similar to that of *Echinocorys* and the Spatangidæ, is well developed on the inner surface of the madreporic genital. In the same genus, in adult specimens, a double row of hemispherical prominences occurs, partly encircling the inner part of the test a little above the ambitus. Klinghardt (**68**) has recently discussed the relation of these thickenings to the course of the alimentary canal, for the mesenteries of which they seem to have given attachment. He has compared the course of the gut thus indicated with that of several fossil and recent species of Spatangidæ. In the present state of our knowledge, however, but little of importance can be ascertained of the comparative anatomy of the soft parts of fossil Echinoids.

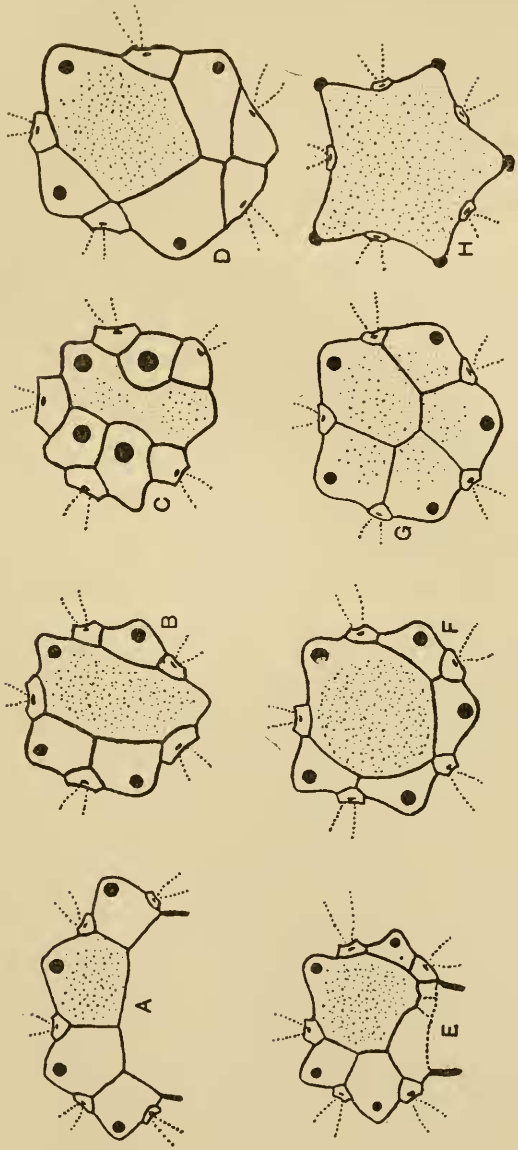
H. The Apical System.

Much of the systematic work that has been done on the Irregular Echinoids has had as its basis the character of the apical system. Notable cases where this feature has been utilized for the purposes of classification are the works of Gaudry ('Enchaînement du Monde animal') and Pomel. From a purely morphological standpoint the system has been carefully described by Lovén (**31**). In the case of the Holectypoida, and of some of the near allies of that group, I have recently summarized the state of our knowledge of the apical system (Hawkins, **70**) in a paper that was definitely a preliminary note to the present work. In consequence, only the comparative aspect of the subject need be dealt with here, and for the description of details that paper may be consulted.

The apical system is at first thoroughly disorganized in its composition and structure by the passage of the periproct through its cycle of plates. In *Pygaster* sens. str., the first stage of disruption is still visible. The posterior genital plate is entirely absent, and the remaining four genitals are grouped in a roughly semicircular order around the anterior edge of the periproct. The madreporic genital is not much larger than the other three. The oculars are small, and show no features of special importance. From a broken and open condition such as that shown by *Pygaster* sens. str., the processes of evolution work along two definite directions. The first aims at a restoration of a cyclic, or at least of a compact, character in the system as a whole, and the second is concerned with the infilling of the centre of the system (when the cycle is regained) to replace the absent periproct.

In the reconstruction of the cycle of genital plates, the posterior (fifth) genital is not necessarily resuscitated. In fact, a very large number of the great groups of the Irregular Echinoids are permanently without this plate. *Anorthopygus* shows the simplest condition of the cycle-restoration on this plan. In that genus the postero-lateral genitals close in, so as to bring the system to an

Text-fig. 59.



The apical system of some Holectypoids and their allies. (Reduced to a common size, but correct in proportion.)

A. *Pygaster* sens. str. B. *Anorthopygus.* C. *Spatangus.* D. *Conulus.* E. *Pygaster* (*Megapygus*). F. *Cœnholectypus.* G. *Discoidea* (the posterior genital pore not invariable). H. *Clypeaster.*

approximately circular shape, and the place of the posterior plate is taken by a prolongation of the madreporic genital through the system. This great increase in the size and extent of the right anterior genital achieves two results. Firstly, the interior of the apical system is filled by it (with the madreporite), and secondly, the posterior margin of the system is completed by its extension. The resulting structure is an apical system of the ethmolysian type (see Gregory, **50**). The great importance of this character in *Anorthopygus* becomes evident when it is realized that such a system is found only in it and in a section of the Spatangidæ. It may be stated at once that the method of infilling of the centre of the system shown in this genus is characteristic of all those Holectypoida in which the apical plates regain a genuinely cyclic arrangement.

The second method whereby the system is rendered compact, without the redevelopment of the posterior genital plate, is shown by *Conulus*. Here the two posterior oculars become greatly increased in size, and meet along the posterior margin of the system. The postero-lateral genitals undergo a similar transverse extension to a greater or less degree, and meet above them. The madreporic genital, although large and partly occupying the centre, is in this way separated from the posterior region of the system. A slight antero-posterior lengthening of the whole system usually accompanies this method of development, and, in a simple sequence indicated in my recent paper, the markedly elongate apical systems of a *Pyrina* and a *Holaster* can be readily derived. The *Conulus*-plan is characteristic of the apical systems of many Jurassic Nucleolitidæ, although it is not the only type developed in that complex series of forms.

Of the type of apical system in which the fifth genital is re-developed (or perhaps replaced by a new but similar plate), *Pygaster* (*Megapygus*) shows the first stage. Here one small plate, perhaps more, imperforate and in all probability flexibly united to the others, makes its appearance at the adapical extremity of the periproct. It seems probable that this new genital plate is a specialized member of the anal series which has become incorporated into the apical system. In *Megapygus* it is always small and imperforate. The next stage in recovery is seen in *Holectypus* sens. str. In this genus the fifth genital is present as a recognizable unit of the genital cycle. It is always smaller than its four associates, however; and of these, the madreporic genital is very large, occupying all the central part of the system. The posterior genital is still imperforate. In the succeeding series of forms (*Cœnholectypus*) the relations of the genital plates are similar to those in the earlier subgenus; but a genital pore, quite as large as those of the other plates, passes through the posterior genital. *Cœnholectypus* shows, then, the perfect restoration of the apical system. All five genital glands will have been functional, each with a separate pore; while the centre of the apical system is filled by the madreporite, situated, as usual, entirely on the right anterior genital plate.

The apical system of *Discoidea* is particularly interesting. The fifth genital becomes practically indistinguishable, in point of size, from the others of the cycle, even the right anterior plate being much reduced from its condition in *Holectypus*. The posterior plate may or may not be perforated, this irregularity affording in itself ample proof of the plastic condition (in a variational sense) of the genus. The madreporite, instead of being restricted to the right anterior genital, is more or less uniformly distributed over all five of these plates in some species, a feature never found in the preceding genera. (In the case of an otherwise abnormal *Conulus albogalerus*, a similar development exists : see Hawkins, **70**.) The oculars have dwindled considerably in proportional size.

The chief interest of this peculiar structure is seen when a comparison is made between the apical systems of *Discoidea* and *Clypeaster*. In the latter genus the madreporite is central and prominent, but it is quite impossible to distinguish the sutures of the genital plates, at least in adult forms. The oculars are minute. *Discoidea*, then, shows the preliminary stages of the assimilation of the genitals—a phenomenon that is preparatory to their coalescence and fusion in the Clypeastroida.

V. The Internal Evolution of the Order.

1. Features of Phylogenetic Importance.

In palæontological attempts to trace a phylogenetic sequence through any series of organisms, the first and essential feature to be considered is the order in time in which the various forms appear. Most of the serious errors that have marred the value of some past work in this direction have resulted from an insufficient reliance on the stratigraphical relations of the genera considered. It is true that our knowledge of the occurrence of fossils at various horizons is very inadequate : it is only necessary to consider the number of cases where a gap exists in the sequence of forms that are known to occur in widely separated horizons, to realize this incompleteness of our knowledge. But it seems a fair postulate to assume that the order in which various genera make their appearance is approximately the true sequence of their evolution. Especially is this the case in the Holectypoida. Not only are they, in common with most Echinoidea, eminently adapted for preservation in suitable deposits, but the periods of their existence, the Jurassic and the Cretaceous, were times when, at least in this country, the conditions of deposition were exceptionally favourable for the preservation of organic remains. In the scheme of evolution put forward below, no apparent relationship has been accepted unless the stratigraphical evidence confirmed it.

A second great principle from which reliable evidence of genetic affinity can be deduced is that of Ontogeny. Here, unfortunately, our knowledge of the Holectypoida is meagre. In the Echinoidea generally the process of recapitulation is always very much obscured by the existence of a free-swimming larval stage. Of post-larval changes in the Class but little is known. Agassiz (30), in the Revision, summarized the state of knowledge of the "young stages of *Echini*," and but little has been added since that date, at least in the case of the Irregularia. Ontogenetic characters are always difficult to observe and to appreciate among fossil forms, and far more zonal collecting of young stages of the Jurassic and Cretaceous Echinoids will be necessary before this line of evidence can be used for their correlation.

Some slight details are available at present, such as the *Hemipedina*-phase of *Pygaster semisulcatus* and the young stages of *Conulus* with an adapical periproct. (Valette, 69, has described a young specimen of *C. subconicus* in which the periproct is already in the adult position, although the individual has a diameter of only 10 mm.). Unlike the Mollusca and Brachiopoda, the Echinoidea do not retain the first-formed portions of the test throughout life; so that, although new parts are continually being developed, the acceleration by which these new portions assume adult characters almost nullifies any recapitulatory features they may possess. In the matter of the interambulacral tuberculation, which at first seems a promising structure for ontogenetic study, this feature of acceleration renders the characters of the new plates practically worthless.

In addition to their sequence in time, it is therefore necessary to consider the adult characters of each genus separately. The features of an adult are divisible into two kinds. The first group is that of adaptation to circumstances; and the characters due to this tendency, though interesting from other standpoints, have little phylogenetic meaning. The second group of characters are those which are unaffected, or are not necessarily affected, by the surroundings of the organism, and which must in consequence owe any peculiarities they possess to the line of evolution of the group to which the individual belongs. Such features, which include atavistic and vestigial structures, are of first-rate importance for showing the phylogeny of a group. In the Echinoidea, the characters that would fall into the first category would be those directly concerned with assimilation, respiration, reproduction, and locomotion. The characters of the second type would consist of apparently trifling variations in the ornament or structure of the test—variations of such a kind as not to affect the vital processes to any serious degree, nor be affected by them. Such characters are the details of the plating of the ambulacra and the variations, within certain limits, in the structure of the apical system. These two characters are regarded as essential indices of relationship in the present paper.

There is, however, in the investigation of an extinct, annectant group like the Holectypoida, an additional principle of evolution that gives safe guidance. The two extremes of structure—those of a Cidarid and of a Spatangid—are known. Generally speaking, the Holectypoida should show a gradual tendency, in the course of their evolution, to depart from the characters of a Cidarid, and to approximate to those of the Irregular types. A recognition of this *direction of evolution* in the group renders the interpretation of the various structures more intelligible by including them all in one coherent scheme. A complete reliance on this principle would probably result in a misinterpretation of degenerate or retarded development, so that the trend of evolution must be considered in direct connection with stratigraphical evidence.

To sum up, the characters used here as indices of phylogenetic development are of two kinds. One series is available for tracing the evolution of the group as a whole. Such features are (i.) the gradual loss of masticatory structures and of peristomial branchiæ, (ii.) the backward movement of the periproct, (iii.) the loss of radial symmetry, and (iv.) the increase in density, and decrease in coarseness, of the tuberculation. The other series is used to indicate the intimate relations of the individual genera of the group. These features are (i.) the plating structure of the ambulacral areas, (ii.) the composition of the apical system, and (iii.) the stratigraphical sequence.

2. The Origin of the Group.

The oldest known member of the Holectypoida is *Pygaster reynesi*, which occurs in the Middle Lias of France. It will therefore be necessary to look for the ancestor of this typically Holectypoid form among the Regular Echinoids of the Liassic or Triassic periods. It is unfortunate that the origin of the group should date from these periods, for, unlike the purer waters of the Oolitic seas, the muddy shore-lines of the Liassic ocean, and the saturated lagoons of the Triassic coral-reefs, were unfavourable to the free development, as well as to the ultimate preservation, of Echinoids. However, it is significant to find that the earliest Irregular Echinoid appeared so soon after the first stage of differentiation had begun among the Regular orders. Its inception thus seems to have been an effect of that unrest in structure and habit that usually accompanies profound changes in the course of the evolution of a Class.

The Liassic Regular Echinoidea seem to belong to two orders only, the Cidaroida and the Diademoida. The former group had become more or less stereotyped in character during the Permian and Triassic periods, having been, as Bather (**59**) indicates, the only surviving member of the varied Palæozoic types. The Diademoida, as the same author has shown (*t. c.*), were beginning to assume the typical features of the order in Triassic times, but still retained features, such as a primary character of the ambulacral plates in the greater part of the area, and a shallowness of the branchial clefts, which are reminiscent of their Cidaroid ancestry.

From the Lias a considerable number of primitive Diademoida are known, and they have been recently studied by Lambert (**52**), Tornquist (57), and Bather (59). A great part of their ambulacra is still built of primaries, which show no signs of their subsequent modification except in the arrangement of the primary tubercles, one to each group of three ambulacrals. A large number of these Liassic forms are grouped under the generic names of *Diademopsis* and *Hemipedina*. These genera and their Diademoid allies have been so exhaustively studied by Bather (*t. c.*) that no detailed discussion of their characters or affinities is necessary here. One of the most obvious features which separate these early Diademoids from their descendants is the structure of the perignathic girdle. The processes, although well developed, are rendered quite inconspicuous by the considerable elevation of the ridges. The latter structures are, of course, a relic of Cidarid characters. This shows that the change from an interradial to a radial position for the perignathic prominences was a gradual one. The view that the increasing complexity of ambulacral structure is connected with the growth of the perignathic processes, which hinder the passage of the ambulacrals on to the peristomial membrane, is supported by Bather (*t. c.*) on this evidence.

There are, then, two orders of Echinoidea from which, on stratigraphical evidence alone, the Holectypoida may have been evolved. Of these orders, the Cidaroida were well established, with their special structures stereotyped, before there is any evidence of the existence of Irregular Echinoids. This fact alone would seem to render unlikely any hypothesis which regarded the early Cidaridæ as directly ancestral to the Holectypoida.

When consideration is taken of the essential features of a *Pygaster*, a notable correspondence between them and the structures of the early Diademoida becomes apparent. The ambulacra are chiefly composed of primaries (with a triple arrangement of tubercles), and towards the peristome a partial compression of the plates into triads is seen. Triad formation, in the same part of the ambulacra, is characteristic of all the early Diademoids, and is one of the diagnostic features of the whole order. The perignathic girdle of *Pygaster* shows well-developed processes, but hardly appreciable ridges. This character, the absolute antithesis to that of the Cidaridæ, is known to have been gradually attained by the Diademoids through their Triassic and Liassic representatives. Again, the apical system of *Hemipedina* often shows a prolongation backwards into the posterior interambulacrum.

Most significant of all is the indication of affinity between the two orders by the slight ontogenetic evidence already available. In discussing the affinities of *Hemipedina bonei*, Wright (20) admitted that he was uncertain as to the true generic relations of the species. He was at one time inclined to class it with *Pygaster*. Bather (59) has referred to this species, and is of the opinion that *H. bonei*, if it is not a *Hemipedina*, should be associated with *Pygaster*. The species is a small one, and the shape of the scar left by the apical system indicates a considerable backward prolongation of that structure. I have before me a series of ten specimens from the Pea Grit of Crickley Hill (near Cheltenham), which are presumably the young of *Pygaster semisulcatus*; but I am unable to find any satisfactory distinctions between them and the type of *H. bonei*. If there is any appreciable difference, it consists in the fact that the periproct does not project so far into the posterior interambulacrum in the *Pygasters* as does the "scar of the apical disc" in the *Hemipedina*. It seems hardly possible that, so early in the history of both orders, heterogenetic homœomorphy could have reached such a degree of perfection, and I am therefore strongly of the opinion that "*Hemipedina*" *bonei* is a *Pygaster*, and almost certainly a young form of *P. semisulcatus*.

It thus seems established that *Pygaster* is intimately related to some primitive, probably Liassic, Diademoid. It is impracticable, in the present state of our knowledge, to search for the actual *generic* ancestor; but if the choice were to lie between *Diademopsis* and *Hemipedina*, the former would seem to possess the stronger claim to recognition. As defined by Lambert (52), *Diademopsis* is distinguished from *Hemipedina* by the presence of pronounced secondary tubercles in the interambulacra. Bather (59) has shown that the distinction is not so absolute as Lambert's diagnosis would suggest, but the fact remains that, among the earlier species of the genera, there is a more strongly developed tendency to a multituberculate character in *Diademopsis*. As *Pygaster* is also a multituberculate form, the alliance with *Diademopsis* would seem natural, but I do not feel justified in expressing a positive opinion on the matter, beyond the statement that the immediate ancestor of the Holectypoida must surely have been a Diademoid.

3. The Pygasteridæ and Conulidæ.

The three subgenera of *Pygaster* sens. lat. mark three stages in the evolution of that genus. *Pygaster* sens. str. is undoubtedly the most primitive type. *Megapygus* shows an advance in two directions. The periproct is undergoing a change of shape preliminary to its actual separation from the apical system, and the tuberculation is assuming slight irregularity of arrangement. Both these features point towards "Irregularity." *Macropygus*, which appeared at about the same horizon as *Megapygus*, shows a similar character in its periproct, but the tuberculation, instead of becoming superficial and irregular, shows a deepening of the scrobicules, and a corresponding reduction of the miliary surface. The distinction from the *Megapygus umbrella* group is not very great in appearance, but seems important in its results. I regard the two subgenera as parallel lines springing from the common ancestor *Pygaster* sens. str.

Pileus is undoubtedly a short-lived offshoot from the *Pygaster*-

stock, for the anomalous biserial ambulacra are unlike any other genera of the order. The periproct position shows an advance on the *Megapygus*-condition, and, owing to certain irregularities of the tuberculation, I am inclined to regard *Pileus* as a side-branch of that line. *Anorthopygus*, which in the classification I have associated with *Pileus*, seems to show a course of evolution parallel with, although in many ways differing from, that of the aberrant genus. The oblique position of the periproct does not appear to be an important character, although peculiar. The tuberculation is definitely like that of *Macropygus* in structure, though not in arrangment, and therefore I have regarded it as an offshoot from that subgenus in Lower Cretaceous times, which corresponded with the similar offshoot from the *Megapygus*-line in the Upper Jurassic.

At about the same horizon in which *Anorthopygus* occurs, *Conulus* appears. The earlier species seem very difficult to distinguish from those of *Pyrina* with which they may be stratigraphically associated. In the matter of the tuberculation the adoral surface of *Conulus* shows much the same characters as the whole test of *Anorthopygus*. Moreover, the arrangement of the tubercles is similar in both genera. The periproct has passed to the posterior edge of the test, although in many young specimens of *C. subrotundus* (some of which are almost globular), the aperture is on the adoral surface quite near to the apex. The feature which marks off *Conulus* so sharply from the Pygasteridæ is the accelerated condition of the ambulacral plate-crushing. There is no appreciable tendency to increase the number of demi-plates in the Pygasteridæ, from the few adorally situated ones, which were probably directly inherited from the Diademoid ancestor. However, in many other features *Conulus* shows almost equal acceleration. When the Upper Chalk is reached, the genus disappears suddenly after a short existence, during which few important specific modifications were evolved. Its relations to the Pygasteridæ are not very easy to decide, but, on the character of the tuberculation, I have connected it with the *Anorthopygus*-line. An additional link between the genera is afforded by the structure of the apical system, the fifth genital plate being permanently absent from both.

4. The Discoidiidæ.

Holectypus sens. str. appears in the Inferior Oolite in association with *Pygaster* sens. str. It is only in the position of the periproct that considerable acceleration is shown, but the differentiation of the characters of the tubercles on the upper and lower surfaces of the test is also a feature of advance. The Holectypinæ are a perfectly homogeneous group, and must be regarded as an unbroken series. *Coptodiscus* is apparently a peculiarly specialized offshoot from *Cœnholectypus*, and the suturing of the adapical surface may perhaps be ascribed to gerontic degeneration of armour (see Oswald, 61). *Lanieria* is also allied to *Cœnholectypus*, but, unlike most of the Holectypinæ, is almost globular in shape. The position of *Discholectypus* is more difficult to determine. In every obvious feature it is a true Holectypine, but it shows an ambulacral structure closely resembling that of *Conulus*. The absolute contrasts of tuberculation, periproct-position, apical structure, and general form which appear when *Discholectypus* and *Conulus* are compared, preclude any possibility of a genetic connection between the genera. *Discholectypus* would seem, therefore, to be a branch of the *Holectypus*-line, which developed complex ambulacral plating by a process of acceleration. This parallelism of development (heterogenetic homœomorphy) of a feature in two distinct genera is rendered particularly interesting by the correspondence *in time* at which the specialization took place.

There can be no doubt as to the close relationship which exists between *Discoidea* and *Holectypus*. On stratigraphical evidence, and also because of the variable nature of the apical system (in the matter of the perforation of the posterior genital plate), I have considered the Discoidiinæ as descendants of *Holectypus* sens. str., whose appearance coincided in time with the modification of the parent stock into *Cœnholectypus*.

5. Summary of Internal Evolution.

The Holectypoida originated from a Diademoid ancestor in the Triassic or early Liassic periods, and subsequently developed along two definite lines. In one line (Pygasteridæ and Conulidæ) the apical system never fully regained, and finally lost, the posterior genital plate, while the whole system tended to become elongated; the tuberculation gradually became uniformly distributed over the interambulacra, and irregular in its arrangement; the shape of the test showed various departures from radial symmetry; and the jaw-structures dwindled and ultimately almost disappeared in adults. In the other line (the Discoidiidæ), the fifth genital plate was early redeveloped, and later regained its function, while the system as a whole became circular in shape; the tuberculation retained its regularity of arrangement, but became insignificant adapically and coarse adorally; the shape of the test eventually regained a radial symmetry; and the jaws, though modified, showed little or no decrease in power.

VI. The External Affinities of the Order.

The primitive character of the early Holectypoida (in an Irregular sense) is so pronounced that it would naturally be expected that the group existed for some time before any of the more elaborate forms were evolved, and that these appeared at subsequent intervals as offshoots from the Holectypoid stock. Such, however, was not quite the case. The Holectypoids are merely a retarded series of Irregular Echinoids, and some of the orders of that subclass early became differentiated from the Pygasteridæ by a relatively accelerated evolution. It is becoming increasingly manifest that large groups of organisms, such as the Irregular Echinoids, are not often homogenetic in the strict sense of the word. When a series of forms that have been regarded as belonging to an individual genus can be shown (as Beecher and others have proved for some Brachiopoda) to pass through widely divergent lines of ontogenetic (and therefore phylogenetic) development, the problem of the evolution of a class or subclass must be considered more complex still. Indeed, at first sight, it would seem that, without the evidence of Ontogeny, no reliable clue to genetic relationship can be deduced from even the most accurate correspondence of adult characters.

Stratigraphical palæontology, however, shows a kind of extended ontogeny which, although fragmentary, is infallible so far as it can be understood. The same phenomena which complicate the study of recapitulation in recent species are as widely developed among the families and orders of past periods. Acceleration and retardation, adaptation and degeneration, tend to obscure the true sequence of genetic affinity to such a degree that, in the present state of knowledge, only the bare outlines of the evolution of the larger groups can be indicated.

In this section of the paper, an attempt is made to show the affinities (with persistent regard to stratigraphical relations) which appear to link certain genera of the Holectypoida with those of other orders. Little account is taken of the subsequent changes which may have been developed in these other groups, and no opinion is expressed as to their absolutely homogenetic characters. The name of a fairly primitive member of each main group is inserted in the diagram (text-fig. 60, p. 493) in its true stratigraphical position, and by a thin vertical line each of these names is connected with that of a characteristic genus now living, which is usually regarded as belonging to the same group.

1. *Pygaster* and *Galeropygus*.

Galeropygus appears in the Upper Lias with at least two species, one of which (*G. dumortieri* Paris) is British. The genus is thus contemporaneous with *Pygaster* sens. str. Gregory (50), probably on account of its obviously primitive characters, included it among his Pygasteridæ, although in almost every feature it offers a violent contrast to the diagnosis of that family. Practically the only diagnostic character in which it resembles an Holectypoid is the apetaloid nature of its ambulacra. A feature which would tend to connect it with some of the later *Pygasters* (e. g., *Macropygus truncatus*) is the shape of the test, which is commonly rather broader than long. The deep anal sulcus finds a shallow counterpart in the posterior interradius of *Pygaster semisulcatus*, but I have indicated above (p. 465) that this sulcus is probably due to the presence of the periproct near the apex, and has, in consequence, little direct phylogenetic meaning.

Galeropygus may be regarded as differing from *Pygaster* sens. str. by a marked acceleration in the characters of its tuberculation and peristome. The former feature is already in the uniform condition, no definite order of appearance being traceable for individual tubercle series. The peristome is quite small, and slightly excentric anteriorly, with no visible adaptation for jaws. I regard the genus as a primitive member of the *Nucleolites*-group, with all the characters of that group except the subpetaloid ambulacra. As there is a marked tendency to develop this feature even among the Holectypoida, it seems that its production in the descendants of *Galeropygus* could be naturally postulated. Owing to the stratigraphical appearance of *Galeropygus*, I should consider it an offshoot from the Diademoida that hardly, if at all, progressed along the Holectypoid line of descent before developing striking acceleration in all its characters except the periproct and the ambulacra. It is interesting to find that the position of the periproct remained more or less constantly primitive in the majority of the Jurassic descendants of *Galeropygus* (e. g., *Echinobrissus* and *Clypeus*), although the ambulacra early began to show elaboration. In the periproct feature, indeed, the Pygasteridæ show a greater acceleration than the Nucleolitidæ, although the Holectypoida are, in most characters, a retarded group.

Even if the affinity between *Galeropygus* and *Pygaster* were to be proved to be less close than I have indicated in the diagram, the characters of the ambulacral plating would show that it was derived, directly or indirectly, from a Diademoid ancestor. As I interpret the relations of the genera at present, *Galeropygus* and *Pygaster* stand together at the root of all the Irregular Echinoids, in structure as well as in stratigraphical position. The subsequent modifications of the *Galeropygus* stock I have briefly outlined in a recent paper (Hawkins, **66**), and I hope to amplify that re-adjustment of the classification of the "Cassidulidæ" at some future time.

2. *Pygaster*, *Conulus*, and the Echinoneidæ.

Since its first recognition by Desmoulins (**4**), the genus *Pyrina* has been the occasion of great confusion. The extraordinary similarities that appear when it is compared with *Conulus* make the generic position of species ascribed to them more difficult to determine than their specific distinctions. Such a form as *P. desmoulinsi*, with its elongated ovoid ambitus, is easily distinguishable from a *Conulus*, the species of which are almost, though rarely quite, circular in outline. To restrict the genus *Pyrina* to such elongated forms would, however, result in a very unnatural grouping of the species, and, unless details of the anatomy can be traced, the distinction of a roughly circular *Pyrina* from a *Conulus* becomes almost impossible. Theoretically a *Conulus* should possess vestiges of jaws, and a peculiar type of perignathic girdle; but jaws are very rarely preserved in fossil Echinoids, and *Pyrina* has a somewhat similar series of structures around the peristome. The similarities between the two genera include the shape (generally), the oblique peristome, the position and shape of the periproct, the structure and arrangement of the tubercles, the ambulacral plating, and the composition of the apical system. Added to these there would probably be the presence of vestigial jaws in young individuals of *Pyrina*, since these structures have been found in a small specimen of the more highly specialized *Echinoneus*. An additional difficulty in the separation of species belonging to the two genera results from the fact that both were evolved at about the same time, and flourished side by side during the Cretaceous period.

So many correspondences in important structures cannot point otherwise than to a close genetic affinity between *Pyrina* and *Conulus*, and the only feature that can be considered to exclude the former genus from the Holectypoida is the absence of jaws in the adult state. The presence of these organs in young specimens cannot be considered sufficient evidence for the inclusion of *Pyrina* in the order; for, if vestigial characters are taken into account in classification, by analogy the Mammalia, by reason of their embryonic gills, would have to be classed with the Pisces.

The earliest members of the Echinoneidæ, such as *Nucleopygus*, have the periproct in a supra-marginal position similar to that of *Anorthopygus*. As Lovén (**36**) has shown, a gradual migration of the periproct takes place in this family along an exactly parallel line to that passed through in the Holectypoida, until in *Echinoneus* the anus is in a position similar to that of *Discoidea*. The features of *Desorella* are so little known that it is unsafe to ascribe a definite systematic position to it, and it has been ignored for the purposes of the present work. I have regarded the Echinoneidæ as offshoots from *Pygaster* (*Macropygus*) in Upper Jurassic times, which for some distance followed the *Anorthopygus* branch, and left it simultaneously with the Conulidæ. They were at first distinguished from that family by the accelerated degeneration of their jaw-structures.

3. *Anorthopygus* and the Spatangidæ.

The earliest members of the *Spatangidæ* proper appear in the Lower Cretaceous. They are not very clearly distinguishable from some other groups, especially from the Echinocorythidæ. The structure of the apical system is, however, different in these two families. The system of the Echinocorythidæ is elongate, and has been compared with that of the Collyritidæ. (I have recently shown (Hawkins, **70**) that this structure could easily be evolved from the Conulid type by acceleration.) The Spatangidæ have a compact apical system, which often nearly resembles that of the Conulidæ, but is sometimes ethmolysian—that is, with the madreporic genital extending right through the system to occupy some part of the posterior border. In every case the fifth genital is absent, and this feature alone serves to distinguish a Spatangid from the great majority of the "Cassidulidæ." At first sight there do not seem to be many points of resemblance between *Anorthopygus* and the Spatangidæ. However, the stratigraphical appearance of the two types is the same, and, in the structure of the apical system, *Anorthopygus* shows an ethmolysian character in both the known species. No types of Echinoids other than *Anorthopygus* and some Spatangids have this feature. The position of the periproct in the Holectypoid genus is about midway between the apex and the ambitus, and the same character holds in almost all the Spatangidæ. In several small specimens of *A. orbicularis* that I have seen there is an appreciable increase in the declivity of the test behind the periproct, and I regard this as a rudimentary posterior surface. The plating of the periproct-membrane also shows some similarity in the two groups.

The evidence for their genetic affinity is very slight, but I have ventured to connect the Spatangidæ with the *Anorthopygus* line of descent on account of the apical structure and stratigraphical correspondence.

4. *Conulus* and *Amblypygus*.

Amblypygus is a Tertiary Echinolampid (Duncan (**44**) classed it as an Echinoneid) whose characters are best known from the descriptions of Indian species given by Duncan and Sladen (**39**). The shape of the test, the obliquity of the peristome, and more especially the structure of the ambulacra, all show features of similarity with those of the Conulidæ. The ambulacra are subpetaloid adapically in *Amblypygus* (a marked contrast to all the Echinoneidæ), but in that region, as much as on the adoral surface, the inclusion of one demiplate between two primaries is regularly shown. It is difficult to imagine that this peculiar structure could be evolved independently in heterogenetic genera. The only other form with which *Amblypygus* could be associated by reason of this structure is *Discholectypus*, but, apart from the contrasts which the two genera show in other respects, the stratigraphical sequence is not favourable. As *Amblypygus* is a very primitive type, and one of the oldest known genera, of the Echinolampidæ, I have separated that family from the other "Cassidulidæ," and derived it from the Conulid stock. The later members of the family seem to have reduced their ambulacral structure to a condition of simple primaries; a process that, outside the order of the Holectypoida, seems to have been the usual one adopted.

5. *Conulus* and *Conulopsis*.

A group of Upper Cretaceous Echinoids, which was formerly classed with "*Galerites*," was separated from that genus by

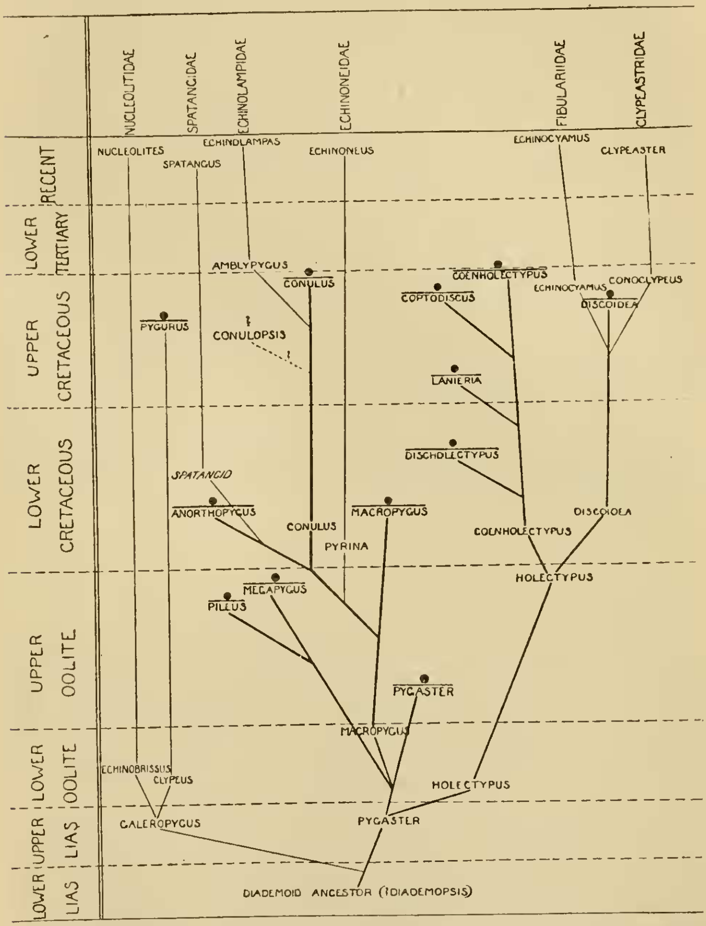
Desor (**21**) under the name of "*Echinoconus*." "*Galerites*" *roemeri* d'Orb., on which the genus was founded, seems to be congeneric with the "*Echinoconus abbreviatus*" and "*orbignyanus*" of the Upper Chalk of Norfolk. The differences between these species and a typical *Conulus* are manifold, and, as the name *Echinoconus* cannot be retained for them, I have distinguished them as *Conulopsis*. The tuberculation of *Conulopsis* is irregular, and the tubercles of the adapical surface have deeply sunken scrobicules. The ambulacra are composed of primaries throughout, the adapical pore-pairs being almost subpetaloid; while round the peristome the interambulacra are raised into definite "bourrelets." The general facies of *Conulopsis* is similar to that of *Caratomus* (the latest discussion of this genus being by Schlueter, **54**). It is possible, however, that some real genetic relation may exist between the later *Conuli* and *Conulopsis*, and that the resemblance of the latter genus to *Caratomus* may be deceptive. Even if *Conulopsis* is a descendant of *Conulus*, it is certainly not an Holectypoid. It would show a development which would have a peculiar interest when compared with the development of *Conoclypeus* from *Discoidea*. The same loss of regularity in the tuberculation is seen, and the ambulacral plates have become restored to their primary state. (The large polygonal ambulacrals of the adoral surface of *Conulopsis* are strikingly similar to those of a *Clypeaster* or of a Spatangid.) The development of a subpetaloid character in the adapical parts of the ambulacra would be comparable in the two genera, while a similar correspondence is shown in the peristomial "bourrelets." Only the position of the periproct (almost marginal in *Conulopsis*), and the presence of strong jaws in *Conoclypeus*, would tend to separate the two genera. These last features would be definitely due to the characters of the ancestor, *Conulopsis* agreeing in them with *Conulus*, and *Conoclypeus* with *Discoidea*.

Conulopsis and *Conoclypeus* would then mark parallel accelerations from different branches of the Holectypoid stock. At present, however, I do not feel satisfied that the genetic connection between *Conulus* and *Conulopsis* exists, but I have connected the two by a broken line in the table.

6. *Discoidea* and the Clypeastroida.

The similarities of structure that link the Discoidiinæ with the Clypeastroida are many and of fundamental importance. A circular outline; an invaginated peristome; an infra-marginal periproct; a madreporite scattered over five genitals, all of which may be perforated by a genital pore; and internal buttresses to the test: are common to most genera of the Clypeastroids, and are diagnostic features in *Discoidea*. The jaws in this genus are strong, in view of its late appearance among the Holectypoida, and, although conforming more to the "Regular" than to the Clypeastroid type, may well have assumed a more expanded shape when the height of the test diminished. The ambulacra in all Clypeastroids are either petaloid or subpetaloid, but *Conoclypeus*, from the Upper Cretaceous, serves to link the simple

Text-fig. 60.



Phylogenetic table of the Holectypoida and their allies. Names of Holectypoid genera are connected by thick lines, those of other orders by thin lines. No details are inserted in groups other than the Holectypoida, the names in the external groups being those of the earliest-known genus that has been satisfactorily described. Short, thick, horizontal lines above names indicate that the genera became extinct at that horizon, and left no direct descendants.

ambulacral pores of *Discoidea* with the more elaborate structures of the later genera. Perhaps, if the jaw-structures of *Conoclypeus* were to be discovered in a more perfect condition than those described by de Loriol (**35**), they also would show an intermediate character. The presence of "bourrelets" round the peristome in this genus are the only features that seem antagonistic to its being regarded as ancestral to the *Clypeaster*-series.

The similarity between the small species of *Discoidea* and *Echinocyamus* caused Gregory (**50**), when revising the unnecessary generic division of "*Echinites*" made by Duncan (**44**), to propose the name *Protocyamus.* The name is inadmissible on systematic grounds, but would be morphologically appropriate. *Echinocyamus* occurs first in the Upper Cretaceous, and has developed but few changes in structure from that time to the present day. H. L. Clark (**64**) has recently suggested that the characters of *Echinocyamus* are not primitive, but rather degenerate. On the stratigraphical evidence I incline to regard them as truly primitive, and to have retained ancestral traits by the retardation of development consequent on their small size.

Echinocyamus (of the Fibulariidæ) was then directly evolved from the smaller (typical) *Discoideæ*, while *Conoclypeus* (of the Clypeastridæ) appeared at the same period as a descendant of (probably) the larger species of *Discoidea* (the "*Pithodia*" of Pomel, **37**). The former group underwent little change in subsequent periods, but the latter became rapidly differentiated into the numerous and complex types that characterize the other families of the Clypeastroida.

VII. Summary.

The Holectypoida are restored to the rank of an order of the Echinoidea Irregularia. A classification, somewhat modified from that proposed by Gregory (**50**), is given, and revised diagnoses of the families, subfamilies, and genera are drawn up. A comparative study of the morphology of the skeletal structures of typical genera of the group is given; and, in the light of the results of this study, the course of evolution both within and beyond the limits of the order is indicated.

The Holectypoida are regarded as an annectant group of the Irregular Echinoids, whose characters retain a considerable uniformity owing to a persistent retardation of evolution. At various periods offshoots from the Holectypoid stock appeared, which, usually with a relatively accelerated differentiation, developed into the various orders and families of the Irregularia. The order commenced in the Liassic period, and became extinct at the end of the Cretaceous. Two of the groups of Echinoids now living retain many features that were characteristic of the Holectypoida (the Echinoneidæ and the Fibulariidæ). The other groups of Irregular Echinoids show a much greater departure from the primitive character, but they all possess some features which indicate their Holectypoid ancestry.

Two new names are introduced in the Systematic Part:—*Megapygus* as a subgenus of *Pygaster*, corresponding with the *Pygaster* (sens. str.) of Pomel (**37**), with type *M. umbrella*; and *Conulopsis*, a genus including the "*Echinoconus*" of Desor (**21**), with type *C. roemeri* d'Orbigny. The latter group will be studied in greater detail in a forthcoming paper.

VIII. List of Literature consulted.

(The numbers of pages and plates in *square* brackets are those which have a special bearing on the subject. Where no such brackets are present, the whole paper has been consulted.)

1. 1734. J. T. Klein.—Naturalis dispositio Echinodermatum etc. [p. 24; Pls. xiii.–xiv.]

2. 1824. C. Stokes.—Extracts from a letter explanatory of three drawings of Echini. Trans. Geol. Soc., ser. ii, vol. ii, p. 406.

3. 1829. J. Phillips.—Illustrations of the Geology of Yorkshire, etc. Part I. [p. 127; Pl. iii. fig. 17.]

4. 1835. C. Desmoulins.—Études sur les Échinides. II. Généralités. Actes Soc. Linn., Bordeaux, Tome vii, pp. 315–432.

5. 1836. E. Grateloup.—Mémoire de Géo-zoologie sur les Oursins fossiles (Échinides) qui se rencontrent dans les Terrains calcaires des environs de Dax. Actes Soc. Linn., Bordeaux, Tome viii, pp. 103–191; Pls. i. & ii. [pp. 140–160; Pl. ii.]

6. 1837. L. Agassiz.—Prodrome d'une Monographie des Radiaires ou Echinodermes. Mém. Soc. Sci. Nat., Neufchatel, Tome i. (Also in) Ann. Sci. Nat., Tome vii (and in) Annals Nat. Hist., vol. i. [p. 302.]

7. 1837. C. Desmoulins.—Études sur les Échinides. III. Synonymie générale. Actes Soc. Linn., Bordeaux, Tome ix, pp. 45–364. [pp. 92–105; 200–363.]

8. 1839. L. Agassiz.—Description des Échinodermes fossiles de la Suisse. Première partie. Spatangoides et Clypéastroides. [pp. 61–94; Pls. vi.; x–xii *bis*.]

9. 1840. L. Agassiz.—Catalogus systematicus Ectyporum Echinodermatum fossilium Musei Neocomensis etc. [pp. 3–7.]

10. 1841. L. Agassiz.—Monographies d'Échinodermes, vivans et fossiles. Echinites. Famille des Clypéastroides. Mon. II. Des Scutelles.

11. 1842. E. Desor.—Id., Mon. III. Des Galérites.

12. 1847. L. Agassiz & E. Desor.—Catalogue raisonnée des familles, des genres, et des espèces de la classe des Échinodermes, fasc. 2. Ann. Sci. Nat., ser. iii, vol. vii, pp. 129–168. [pp. 143–153.]

13. 1849. E. Forbes.—Mem. Geol. Surv., United Kingdom. Figures and Descriptions of British Organic Remains. Decade I. [Pls. vii & viii.]

14. 1850. E. Forbes.—*Tom. cit.*, Decade III. [Pls. vi–viii.]

15. 1852. T. Wright.—On the Cassidulidæ of the Oolites, with descriptions of some new species of that family. Ann. Mag. Nat. Hist., ser. ii, vol. ix, pp. 81–103 et seqq. [pp. 88–98; Pls. iii. & iv.]

16. 1854. G. Cotteau.—Études sur les Échinides fossiles du département de l'Yonne. Tome I. Terrain jurassique. [pp. 194–220; Pls. xxvii–xxxii.]

17. 1855. T. Wright.—Monogr. Brit. Foss. Echinod., Oolitic Formations. Part I. Palæontographical Soc. [pp. 19, 20.]

18. 1856. A. Leymerie & G. Cotteau.—Catalogue des Échinides fossiles des Pyrénées. Bull. Soc. Géol. France, ser. ii, Tome xiii, pp. 319–355. [pp. 329–332.]

19. 1856. J. W. Salter.—Mem. Geol. Surv., United Kingdom. Figs. and Desc., Brit. Org. Rem., Decade V. [Pls. vii & viii.]

20. 1856. T. Wright.—Monogr. Brit. Foss. Echinod., Ool. Form., Part II. Palæontogr. Soc. [pp. 258–290; Pls. xviii–xx.]

21. 1857. E. Desor.—Synopsis des Échinides fossiles. [pp. 161–197; Pls. xxii–xxvi.]

22. 1857. E. Pictet.—Traité de Paléontologie. Edit. II, Tome iv. [pp. 223-229.]
23. 1859. G. Cotteau & —. Triger.—Échinides du département de la Sarthe, considérés au point de vue zoologique et stratigraphique. (1855-1859.)
24. 1859. A. d'Orbigny [posthumous].—Paléontologie française. Terrains crétaces, Tome vi. [pp. 459-550; Pls. 978-1006.]
25. 1860. T. Wright.—Mon. Brit. Foss. Ech., Ool. Form., Part IV, and Supplement. Palæontogr. Soc. [pp. 424-425; 463-464; Pl. xli.]
26. 1861. H. Michelin.—Monographie des Clypéastres fossiles. Mém. Soc. Géol. France, Ser. ii, Tome vii, Mém. 2.
27. 1861. L. Saemann & A. Dollfuss.—Études critiques sur les Échinodermes fossiles du Coral-rag de Trouville (Calvados). Bull. Soc. Géol. France, Ser. ii, Tome xix, pp. 168-184, Pl. iii.
28. 1869. G. Cotteau.—Paléontologie française. Terr. jurass., Tome ix. [pp. 330-363; 384-503: Pls. 86-91; 98-138.]
29. 1871. E. Desor & P. de Loriol.—Échinologie Helvétique. Description des Oursins fossiles de la Suisse. Échinides de la période jurassique. (1868-1872). [pp. 257-301; Pls. xliv-xlvi.]
30. 1874. A. Agassiz.—Revision of the Echini, Part IV. Structure and Embryology of the Echini. Mem. Mus. Comp. Zool., Harvard, No. vii.
31. 1874. S. Lovén.—Études sur les Échinoidées. K. Svensk. Vet.-Akad. Handl., Bd. xi, No. vii.
32. 1874. T. Wright.—Mon. Brit. Foss. Ech., Cret. Form., Vol. I. Echinoidea, Part vi. Palæontogr. Soc. [pp. 198-224; Pls. xlvi-lii.]
33. 1875. P. de Loriol.—Description des Échinides Tertiaires de la Suisse. (Échinologie Helvétique, Partie iii.) Mém. Soc. Pal. Suisse, Tome ii. [p. 80.]
34. 1880. G. Cotteau, P. A. Péron & V. Gauthier.—Échinides fossiles de l'Algérie. Tome II. Terr. secondaires. Fasc. vi, Étage turonien, pp. 1-110: Pls. i-viii.
35. 1881. P. de Loriol.—Monographie des Échinides contenus dans les couches nummulitiques de l'Égypte. Mém. Soc. Phys. Hist. Nat., Genève, vol. xxvii. [pp. 75-85.]
36. 1883. S. Lovén.—On *Pourtalesia*, a genus of Echinoidea. K. Svensk. Vet.-Akad. Handl., Bd. xix, No. vii. [pp. 20-21; 68-70.]
37. 1883. A. Pomel.—Thèses doctorales. Thèse I. Classification méthodique et genera des Échinides vivants et fossiles. Alger. [pp. 67-76.]
38. 1884. P. M. Duncan.—On *Galerites albogalerus* Lamarck, syn. *Echinoconus conicus* Breynius. Geol. Mag., Dec. iii, vol. i, pp. 10-18.
39. 1884. P. M. Duncan & W. P. Sladen.—Description of the Fossil Echinoidea from the Khirthar Series of Nummulitic strata in Western Sind. Palæontologia Indica, Ser. xiv: Tertiary and Upper Cretaceous Fossils of Western Sind. Vol. i, part iii, pp. 109-246; Pls. xxi-xxxviii. [pp. 140-149; Pl. xxvi.]
40. 1886. P. M. Duncan.—On the Perignathic Girdle of the Echinoidea. Journ. Linn. Soc., Zool., vol. xix, pp. 179-212; Pls. xxx-xxxi.
41. 1886. P. M. Duncan & W. P. Sladen.—On the Anatomy of the Perignathic Girdle and of other parts of the test of *Discoidea cylindrica*. *Loc. cit.*, vol. xx, pp. 48-61.
42. 1887. G. Cotteau.—Paléont. franç., Terr. tert., Tome i, Échinides Éocènes. [p. 452.]
43. 1888. S. Lovén.—On a recent form of the *Echinoconidæ*. Bihang K. Svensk. Vet.-Akad. Handl., Bd. xiii, Afd. iv, No. 10.
44. 1889. P. M. Duncan.—Revision of the Genera and great Groups of the Echinoidea. Journ. Linn. Soc., Zool., vol. xxiii, pp. 1-311. [pp. 25; 135-173.]
45. 1889. P. M. Duncan & W. P. Sladen.—Note on the Perignathic Girdle of *Discoidea cylindrica*. Ann. Mag. Nat. Hist., ser. vi, vol. iv, pp. 234-239.
46. 1889. V. Gauthier.—Description des Échinides fossiles recueillis en 1885 et 1886 dans le région sud les Hauts-Plateaux de la Tunisie par M. Phillipe Thomas. Exploration scientifique de la Tunisie.
47. 1891. G. Cotteau.—Paléont. franc., Terr. tert., Tome ii. [pp. 190-393; Pls. 249-259.]
48. 1892. S. Lovén.—Echinologica. Bihang K. Svensk. Vet.-Akad. Handl., Bd. xviii, Afd. iv, No. 1.

49. 1895. G. Cotteau & V. Gauthier.—Mission scientifique en Perse, par J. de Morgan. Tome iii, Partie ii, Paléontologie. Pt. 1, Échinides fossiles. [p. 76; Pl. xii.]
50. 1900. J. W. Gregory.—(in) Lankester's Treatise on Zoology. Vol. iii, Echinoderma, Chap. xv, Echinoidea. [pp. 315–321: 328.]
51. 1900. E. Hesse.—Die Mikrostructur der fossilen Echinoideenstacheln und derer systematische Bedeutung. N. Jahrb. f. Min., Stuttgart, Beilage-Band xiii, pp. 185–264; Taf. xii & xiii.
52. 1900. J. Lambert.—Étude sur quelques Échinides de l'Infra-Lias et du Lias. Bull. Soc. Sci. hist. nat., Yonne. Semestre I, Partie 2, pp. 3–57; Pl. i, Tab. A & B.
53. 1900. W. P. Sladen.—(in) Zittel-Eastman, Text Book of Palæontology, Vol. I. (Echinoidea). [pp. 233–239.]
54. 1902. C. Schlueter.—Zur Gattung *Caratomus*. Zs. D. Geol. Gesell., Bd. 54, pp. 302–335; Pls. xi & xii.
55. 1905. F. A. Bather.—The Echinoid name *Discoidea subucula*. Ann. Mag. Nat. Hist., ser. vii, vol. xv, pp. 145–148.
56. 1908. E. T. Paris.—Notes on some Echinoids from the Lias of Worcestershire, Gloucestershire, and Somerset. Proc. Cottesw. Nat. F. Cl., vol. xvi, part 2, pp. 143–150. [p. 149.]
57. 1908–9. A. Tornquist.—Die Diadematoiden des wurttembergischen Lias. Zs. D. Geol. Gesell., Bd. 60, pp. 378–384; Pls. xv–xix (1908); pp. 385–430 (1909).
58. 1909. A. Agassiz.—On the existence of Teeth and of a Lantern in the genus *Echinoneus* Van Phels. Amer. J. Sci., ser. iv, vol. xxviii, pp. 490–492; Pl. ii.
59. 1909. F. A. Bather.—Triassic Echinoderms of Bakony. Result. Wissensch. Erforsch. des Balatonsees. Bd. I, Teil i, Pal. Anhang. [pp. 108–113.]
60. 1909. H. L. Hawkins.—On the Jaw-Apparatus of *Discoidea cylindrica* (Lamarck). Geol. Mag., Dec. v, vol. vi, pp. 148–152; Pl. vi.
61. 1909. F. Oswald.—The Degeneration of Armour in Animals. Science Progress, No. xiii, pp. 123–134.
62. 1910. H. L. Hawkins.—Some Ambulacral Structures in the Holectypoida. Geol. Mag., Dec. v, vol. vii, No. 554, pp. 349–353.
63. 1910. W. Loescher.—Die westfälischen Galeritenschichten mit besonderer Berücksichtigung ihrer Seeigelfauna. N. Jahrb. f. Min., Beilage-Band xxx, pp. 269–312.
64. 1911. H. L. Clark.—The genera of Recent Clypeastroids. Ann. Mag. Nat. Hist., ser. viii, vol. vii, pp. 593–605. [p. 601.]
65. 1911. H. L. Hawkins.—On the Teeth and Buccal Structures in the genus *Conulus* Leske. Geol. Mag., Dec. v, vol. viii, pp. 70–74; Pl. iii.
66. 1911. H. L. Hawkins.—On the Structure and Evolution of the Phyllodes in some fossil Echinoidea. *Tom. cit.*, pp. 257–265; Pl. xiii.
67. 1911. H. L. Hawkins.—On the Tuberculation of the Holectypoida. *Tom. cit.*, pp. 442–454.
68. 1911. Fr. Klinghardt.—Ueber die Organisation und Stammesgeschichte einiger Irregulärer Seeigel der Oberer Kreide. Jena. Pp. 1–27; Pls. i–xiii.
69. 1911. A. Valette.—Description de quelques Échinides nouveaux de la Craie. (Supplement.) Bul. Soc. Sci. hist. nat., Yonne. Semestre II (1910) pp. 121–151. [pp. 147–149.]
70. 1912. H. L. Hawkins.—On the Evolution of the Apical System in the Holectypoida. Geol. Mag., Dec. v, vol. ix.